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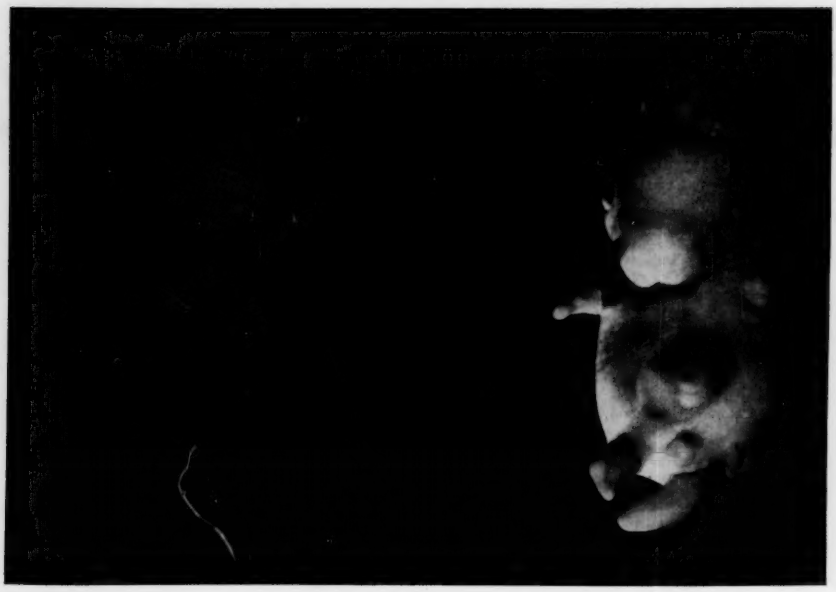

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Loose Pericarp in Corn

Female Sterility in Sorghum

The Florida Guinea Cow—A Dexter Type?

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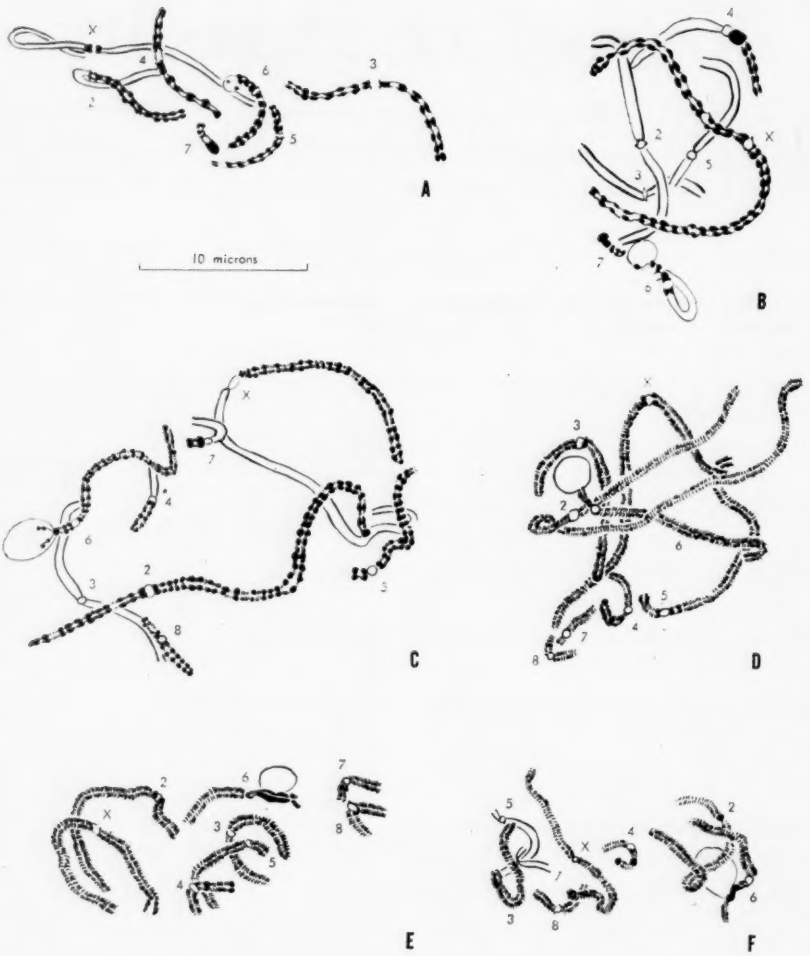


PACHYTENE CHROMOSOME COMPLEMENTS OF MALES

Figure 1

A and *B*—*Schistosomatium douthitti*. *C* and *D*—*Ornithobilharzia canaliculata*. *E* and *F*—*Schistosoma mansoni*. × 2550.

PACHYTENE CHROMOSOMES IN THREE SPECIES OF SCHISTOSOMES

Sex and Autosomal Bivalents in Males and Females

MARGARET Y. MENZEL AND ROBERT B. SHORT*

IT IS well known that blood flukes of the family Schistosomatidae are dioecious, in contrast to the hermaphroditic condition of the vast majority of trematodes. The marked sexual dimorphism of adults and its absence in larval stages, as well as the medical importance of some species, has stimulated study of the mechanism of sex determination in the family.

It has been shown[10, 11, 12] that females of *Schistosomatium douthitti* and *Ornithobilharzia canaliculata* are heterogametic and that a heteromorphic pair of sex chromosomes can be identified at mitotic metaphase. The first cytological studies[2, 5, 9] of the human blood flukes, genus *Schistosoma*, suggested a multiple sex-chromosome mechanism with the males heterogametic. More recent studies[4, 8, 12], however, failed to show any difference in chromosome complement between males and females in three species of this genus. Both sexes have $2n = 16$ and identical mitotic karyotypes.

The present study deals with the pachytene chromosome complements in males and females of *Schistosomatium douthitti* (Cort, 1914) Price, 1931; *Ornithobilharzia canaliculata* (Rudolphi, 1819) Odhner, 1912; and *Schistosoma mansoni* Sambon, 1907. In a study of oogenesis in *S. douthitti*, Nez and Short[7] found that the chromosomes in the nuclei of primary oocytes reach pachytene in the ovary and that a large proportion of oocytes in the distal coils of the ovary are in this stage. Examination showed that the same situation prevails in *O. canaliculata* and *S. mansoni*. All stages of meiosis, including pachytene, are readily available in testes of the males. Since the chromosome numbers are low and the individual chromosomes can all be identified at mitosis[10, 12], the material appeared to afford an unusually favorable opportunity for comparing pachytene bivalents in both hetero- and homogametic sexes of species with and without differentiated sex chromosomes.

Materials and Methods

Preliminary studies of *S. douthitti* utilized a strain from near Chicago, Illinois. Unless otherwise noted, however, the observations reported here concern a strain obtained in 1957 from near Alanson, Michigan and maintained in the laboratory, using *Lymnea palustris* as the intermediate host. A Puerto Rican strain of *S. mansoni* and its snail host (*Australorbis glabratus*) were supplied by Dr. M. A. Stirewalt. Adult worms of both species were obtained from white mice which had been exposed to cercariae from laboratory-reared experimentally infected snails.

To obtain adults of *O. canaliculata*, pigeons were exposed to cercariae from naturally infected snails (*Batillaria minima*) collected at Tampa Bay, Florida by Dr. L. R. Penner and shipped to this laboratory.

For study of pachytene chromosomes, bisexually infected definitive hosts were killed, and adult worms *in copula* were removed from the blood vessels in warm physiological saline appropriate to the host and fixed in a fresh mixture of 1 part glacial acetic: 3 parts 95 percent

*Department of Biological Sciences, Florida State University, Tallahassee. This investigation was supported by research grant E-1142 from the National Institute of Allergy and Infectious Diseases of the National Institutes of Health, U. S. Public Health Service. Thanks are due to Dr. M. A. Stirewalt for providing the strain of *S. mansoni*, and to Dr. L. R. Penner for furnishing snails infected with *O. canaliculata*. The authors wish to acknowledge the technical assistance of Mr. R. B. Holliman during much of this investigation.

ethanol. After 24 hours, the worms were transferred to fresh acetic alcohol and stored in a freezer at about 0° F, where they could be kept for several months without deterioration.

Preliminary studies of pachytene were made from temporary aceto-carmine squashes of the Illinois stock of *S. douthitti*. The pachytene nuclei were well-spread but very faintly stained. Examination with phase contrast enhanced contrast but failed to permit discrimination between single and synapsed strands. Hence we were at first led to the erroneous conclusion[6] that the XY pair could not be identified at pachytene in *S. douthitti*.

Following a suggestion of Dr. Charles Ray, Jr. of Emory University, the following schedule was adopted for subsequent studies. Worms fixed in acetic alcohol were hydrolyzed for 10 minutes at 60° C in 1N HCl, rinsed in two changes of distilled water, and stained *in toto* for one hour at 60° C in a shell vial containing a few drops of Gomori's chrom-alum hematoxylin prepared according to Gray[3] (p. 291). The stain was then diluted with sufficient distilled water to make the worms visible, the diluted stain was decanted, and the worms were rinsed twice in distilled water and destained in 45 percent acetic acid for five to 20 minutes. Worms were then removed individually to a drop of 45 percent acetic on a slide. The region of the ovary or testes was excised, freed of as much somatic tissue as possible, and squashed. In such preparations, the chromosomes were stained intensely blue against a clear background.

The pachytene nuclei were best in freshly made squashes, and some structural details were confirmed in such preparations. However, since it was desirable to have uniform permanent slides for comparison, the data included here were taken principally from 75 to 100 slides of each species which had been made permanent by the method of Conger and Fairchild[1].

The pachytene idiograms were constructed as follows: Camera lucida tracings were made at a magnification of 5100× of 10 well-spread complete chromosome complements in which the centromere constrictions could be located in all the bivalents. The length of each chromosome segment was measured on the drawings to the nearest millimeter and the average length was calculated and plotted to the scale shown. Individual bivalents of the complement were arranged to correspond to the order adopted for the mitotic chromosomes[12], with the shorter ("left") arm above and the longer ("right") arm below. For Y chromosomes, "left" and "right" refer respectively to the arms which pair with the left and right arms of X.

Mitotic idiograms for nine species of schistosomes, including the three discussed here, have been published elsewhere[12], and references to mitotic chromosomes refer hereinafter to this work unless otherwise stated. For convenience, mitotic idiograms of *S. douthitti*, *S. mansoni* and *O. canaliculata* have been redrawn (Figure 4) to the same scale as the pachytene idiograms. It should be noted that the mitotic and pachytene lengths may not be strictly comparable. The mitotic measurements were made in aceto-carmine squashes, in which the chromosomes are appreciably longer than in hematoxylin squashes. Whether the pachytene bivalents also react differently to the two stains is unknown.

Chromosome regions which stained more intensely than the rest of the complement will be referred to as "heterochromatic," without prejudice as to their behavior at other stages of the chromosome cycle. Regions which did not show distinctive staining will be called "euchromatic" in the same sense.

Observations

Pachytene complements of males and females of the three species are pictured in Figures 1*A-F* and 2*A-F* and represented diagrammatically in the idiograms of Figure 4. Average lengths of the various arms are summarized in Table I.

In unflattened pachytene nuclei, the bivalents have a "bouquet" arrangement, with the nucleolus and the chromosome ends oriented toward a small area on the nuclear membrane. This arrangement is

PACHYTENE CHROMOSOME COMPLEMENTS OF FEMALES

Figure 2

A and *B*—*Schistosomatium douthitti*. *C* and *D*—*Ornithobilharzia canaliculata*. *E* and *F*—*Schistosoma mansoni*. × 2550.

usually disrupted in well-spread nuclei, but some suggestion of it can be seen in, for example, Figures 1*B* and *E*, 2*E* and *F*. The relative chromosome lengths and arm length ratios correspond closely to those of the mitotic complements, but the total lengths of the pachytene complements are at least three to four times the mitotic lengths. The two synapsed chromosomes of a bivalent are often coiled around each other, and the centromere regions appear as gaps or constrictions in which little detail can be discerned. The bivalents have a fuzzy, chromomeric appearance. In *S. douthitti*, the chromomere structure was distinct enough to permit an estimate of the number of chromomeres per arm (Table II; Figures 1*A* and *B*, 2*A* and *B*, 3*A-D*). Figure 1*C* indicates the chromomeric appearance of some of the arms in an unusually favorable nucleus of *O. canaliculata*. The chromomere structure in both *O. canaliculata* and *S. mansoni* was less distinct than in *S. douthitti*, and, with the exception of a few chromosome regions noted below, efforts to count the chromomeres were soon abandoned.

The pachytene complements of each species are characterized below.

***Schistosomatium douthitti* (*n* = 7)**

All the chromosomes could be identified in complete pachytene nuclei (Fig-

TABLE II. Number of chromomeres per chromosome arm at pachytene in *Schistosomatium douthitti* (L = left arm, R = right arm)

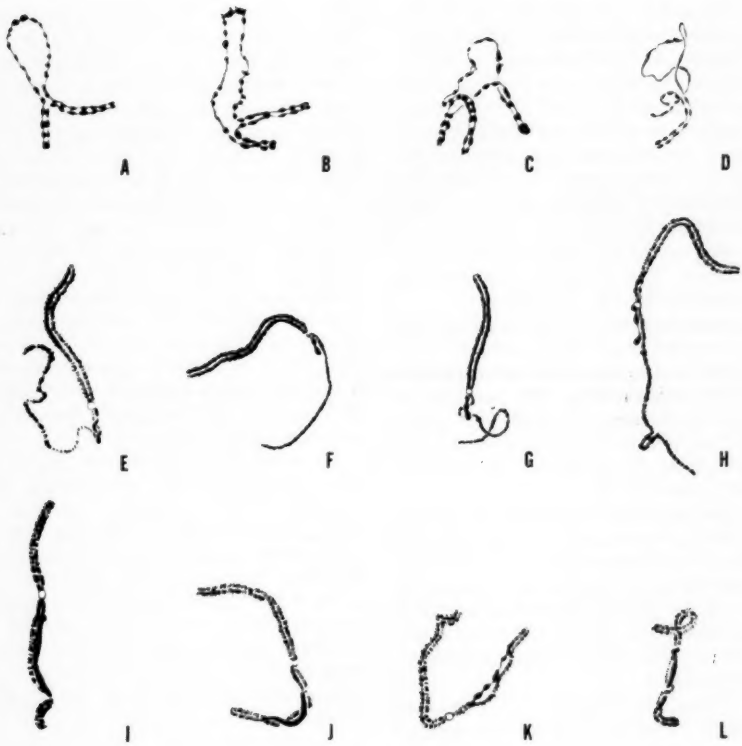
		Females		Males	
Chromosome	Arm	Mean	Range	Mean	Range
Y	"L"*	4	3-4	—	—
	"R"*	8	6-9	—	—
X	L	15	12-18	15	12-18
	R	18	14-21	17	14-23
2	L	10	9-10	9	7-10
	R	11	10-13	11	9-15
3	L	7	7-8	7	5-8
	R	8	7-10	8	5-10
4	L**	5	4-6	5	4-5
	R	7	6-8	6	5-7
5	L	4	3-4	4	3-5
	R	10	8-12	10	7-11
6	L	3	none	3	none
	R	9	8-10	9	7-10
7	L**	0	—	0	—
	R	3	2-4	3	2-3

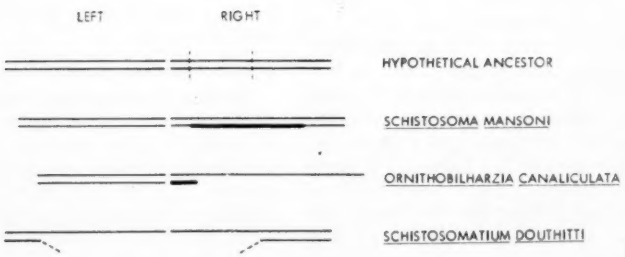
*Chromosome regions homologous with distal regions of left and right arms of X, respectively.
**Excluding the heterochromatic region.

TABLE I. Mean lengths, to the nearest 0.2 micron of chromosome arms at pachytene in three species of schistomosomes (L = left arm, R = right arm)

		S. douthitti		*O. canaliculata*		*S. mansoni*	
Chromosome	Arm	Female	Male	Female	Male	Female	Male
Y	L	6.8	—	8.0	—	6.0	—
	R		—	1.6	—	7.0	—
X	L	10.2	9.2	8.0	9.8	6.0	6.2
	R	10.4	11.0	12.2	15.0	7.0	7.4
2	L	5.0	5.4	6.4	6.0	3.6	3.0
	R	5.6	5.8	15.8	15.6	9.0	9.0
3	L	4.0	4.0	5.4	4.8	4.2	3.2
	R	5.0	5.0	6.6	6.8	5.4	4.2
4	L	3.6	3.6	2.8	2.4	1.8	1.8
	R	4.0	3.8	3.2	2.8	2.0	2.0
5	L	1.8	1.8	1.4	1.4	1.2	1.0
	R	6.4	6.2	7.6	9.0	5.6	4.2
6	L*	1.4	1.0	1.4	1.2	1.4	1.4
	R	5.0	5.0	9.2	8.4	6.0	5.0
7	L	0.8	0.8	0.8	0.8	0.8	0.8
	R	1.8	1.4	4.0	3.2	2.2	2.0
8	L	—	—	1.2	1.0	1.4	1.4
	R	—	—	2.8	2.6	1.8	1.6
Total pachytene length, AX*		65.0	64.2	88.8	90.6	59.6	54.6
Total mitotic metaphase length AX**		21.0		22.4		18.8	

*Excluding region distal to point of attachment of the nucleolus.
**Excluding satellite on chromosome 6, from aceto-carmine squashes, recalculated from data of Short and Menzel[12].





COMPARISON OF XY PACHYTENE BIVALENTS

Figure 3

A-D—XY bivalents of *Schistosomatium douthitti*. *A* and *B*, typical configurations; *C*, non-homologous "foldback" pairing in left arm of X; *D*, terminal region of left arm unpaired. *E-H*—XY bivalents of *Ornithobilharzia canaliculata*. *I-L*—XY bivalents of *Schistosoma mansoni*. *A-L* × 2550. *M*—Relative proportions and positions of pairing and differential segments in X and Y chromosomes of the three species studied and in a hypothetical ancestral stock, ignoring differences in absolute length (X above, Y below).

ures 1*A* and *B*, 2*A* and *B*). In broken cells, chromosomes 2 and 3 are not easily discriminated. Chromosome 2 is slightly longer and averages nine to 10 chromomeres in the left arm and 11 in the right, in contrast to seven and eight chromomeres in the left and right arms respectively of chromosome 3 (Table II). Chromosome 4 is easily identified by a heterochromatic segment about 0.8 micron long in the left arm adjacent to the centromere. The left arm of chromosome 7 is entirely heterochromatic.

In chromosome 6, two or three faint chromomeres were often seen distal to the point of attachment of the nucleolus, probably representing the satellite of mitotic chromosome 6. Since this region was often obscured by the nucleolus and varied greatly in length, no attempt was made to measure it.

In the aceto-carmine slides of the Illinois stock, chromosome 6 frequently had a short heterochromatic segment subtending the nucleolus. In the hematoxylin slides of the Michigan stock this feature was absent. It is not certain whether the difference was one between strains or between stains.

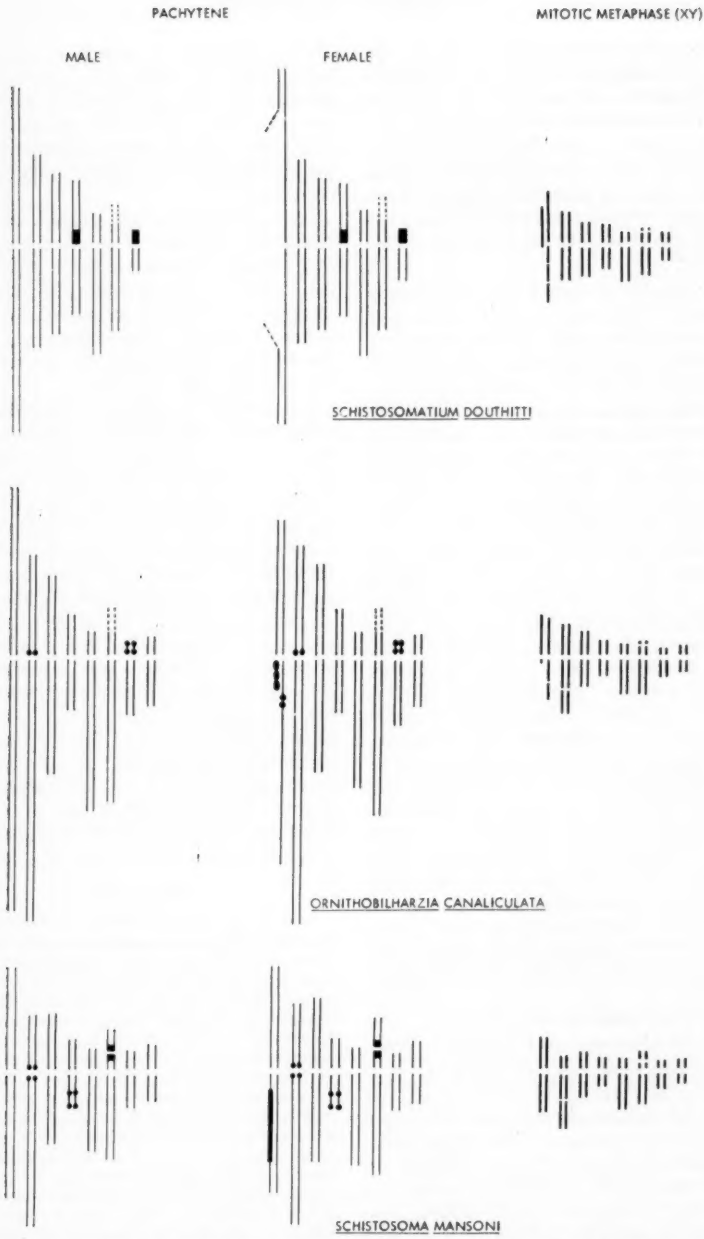
In males, the longest (XX) bivalent is nearly twice as long as the longest autosomal pair and is devoid of distinguishing features other than the centromere, which is median. No differentiated regions corresponding to the marked secondary constrictions in the right arm at mitosis[10, 12] were seen at pachytene.

In females, both X and Y are euchromatic. The Y contains about 12 chromomeres, of which four synapse with the end of the left arm and eight with the end of the right arm of X (Table II; Figures 2*A* and *B*, 3*A-D*). The interstitial region of X, containing the centromere and about 21 chromomeres, forms a large unpaired loop. Occasionally one or more short regions of non-homologous "fold-back" pairing were present in the loop (Figures 2*A*, 3*C*). The centromere of X was clearly visible as a clear area flanked by two rather large chromomeres in the middle of the unpaired region, but no convincing evidence concerning the location of the centromere of Y was obtained. At mitosis, the Y usually appears as a rod, slightly tapered toward the end attached to the spindle. A suggestion of a very minute short arm is sometimes seen at mitotic prophase, but not at metaphase. It seems probable that the Y has a nearly terminal centromere. It is, however, unlikely that it is truly terminal: Observation of 40 metaphase I plates in oocytes (unpublished data) suggested that the XY bivalent usually has a chiasma in each arm of the X. If the centromere of Y were terminal and the chiasmata in both left and right arm of X involved the same arm of Y, all two-chiasma XY bivalents would result in a dicentric and a fragment. No evidence of fragments or of anaphase bridges was encountered at anaphase I or II.

It seems likely, therefore, that Y has two arms, and that the shorter arm regularly forms a chiasma with one end of X. It is tempting to suppose that the centromere lies between the segments of Y which pair with the right and left arms of X respectively. If this were true, however, the shorter arm should be visible at mitosis, since other euchromatic regions with a similar number of chromomeres at pachytene (e.g., the left arms of chromosomes 5 and 6, the right arm of chromosome 7, see Table II) are apparent at mitotic metaphase. It seems more probable that the centromere of Y is located within one of the segments, perhaps only one or two chromomeres from the end.

***Ornithobilharzia canaliculata* (n = 8)**

All the chromosomes could be identified in intact nuclei (Figures 1*C* and *D*, 2*C* and *D*). The bivalents were longer, less deeply stained, and more difficult to spread than in the other two species. Autosomal bivalents in incomplete nuclei often could not be identified. Exceptions were chromosome 2, which has a heavily stained chromomere adjacent to the centromere in the left arm, and one of the two smallest pairs, which has two heavily stained chromomeres in the left arm. The latter was arbitrarily designated chromosome 7. Since both the small chromosomes are heterobrachial at pachytene, whereas one is heterobrachial



IDIOGRAMS OF PACHYTENE AND MITOTIC METAPHASE CHROMOSOMES

Figure 4

All chromosomes × 2550. Somatic complements redrawn from data of Short and Menzel[12].

and the other nearly isobrachial at mitosis, it is uncertain which of the pachytene bivalents corresponds to chromosome 7 of the mitotic karyotype.

The region of attachment of the nucleolus on chromosome 6 is euchromatic. A short segment containing two or three faint chromomeres is present distal to this region, but it defied accurate measurement.

The XX bivalent in males of *O. canaliculata,* like that of *S. douthitti,* lacks any feature corresponding to the secondary constriction in the right arm of the mitotic X (Figure 1*C* and *D*).

The mitotic Y of *O. canaliculata,* unlike that of *S. douthitti,* has a minute but visible short arm; otherwise the two Y's appear similar. The XY pachytene bivalent of *O. canaliculata,* however, differs strikingly from that of *S. douthitti.* The long arm of Y is euchromatic, and synapses with and corresponds exactly to the left arm of X (Figures 2*C* and *D*, 3*E-H*). The short right arm of Y averages about 1.8 microns in length (Table I) and is composed of three elongated heterochromatic chromomeres. It is sometimes unpaired, but usually appears intimately synapsed with the proximal, euchromatic region of the right arm of X. The right arm of X extends beyond the end of Y as a long, euchromatic, often much tangled, single strand averaging about 10.4 microns in length. Frequently one or two heavily stained chromomeres were noted in the right arm of X just distal to the end of Y (Figures 2*D* and 3*H*), although this feature was not seen in the XX bivalents of males.

***Schistosoma mansoni* (*n* = 8)**

All the chromosomes could be identified in favorable cells (Figures 1*E* and *F*, 2*E* and *F*). Chromosome 2 has an intensely stained chromomere on either side of the centromere. The three smallest pairs, 4, 7, and 8, are difficult to discriminate. Chromosome 4 usually has two deeply stained chromomeres, one interstitial and one terminal, in the right arm; chromosome 7 has a submedian and chromosome 8 a nearly median centromere.

The nucleolus is attached to chromosome 6 in the region of (perhaps between) two heterochromatic segments in the left arm (Figures 1*E* and *F*, 2*E* and *F*). The euchromatic region distal to the nucleolar attachment is about one micron long.

The pachytene karyotypes of both sexes are similar in arm length ratios and relative chromosome lengths. In males, all of the bivalents are composed of two identical chromosomes, and the longest bivalent (chromosome 1) lacks distinguishing features in either arm (Figure 1*E* and *F*).

In females, however, chromosome 1 contains an interstitial segment in the right arm in which the two synapsed strands differ in appearance (Figures 2*E* and *F*, 3*I-L*). One of the strands is heterochromatic and the other is not.

The differentiated segment begins about one micron from the centromere and continues for a distance of about 4.4 microns, comprising nearly two-thirds of the arm. Frequently the two unlike strands lay parallel and appeared as intimately synapsed as the remainder of the complement (Figures 2*F* and 3*I*). More often, however, the euchromatic segment seemed slightly longer than and was coiled around its heterochromatic partner (Figures 2*E*, 3*J* and *L*). In a few cases, the differentiated segments apparently were not synapsed (Figure 3*K*).

Discussion

The Y chromosome of *S. douthitti* is apparently completely homologous with the two ends of X. The evidence suggests that chiasmata, and hence crossing-over, occur in both paired segments of the XY bivalent. It seems improbable, therefore, that sex-determining factors are present in these regions, or that Y contains a differential segment or has a strongly female-determining effect. The cytological evidence suggests rather that sex determination in this species depends upon a balance between the autosomes and factors located in the differential segment of X. This interpretation accords with the observation[10] that a triploid of constitution XYY was female, whereas an XXY triploid was male. The Y may be regarded as a deficiency chromosome which has perhaps persisted primarily for mechanical reasons. It is interesting that haploid eggs containing X can initiate parthenogenetic development, occasionally completing larval de-

velopment and producing haploid adult male worms, whereas haploid eggs containing Y have never been found undergoing embryonic development[11]. Thus, in addition to sex-determining factors, the differential segment of X probably contains factors necessary at least to the initiation, if not the completion, of larval development.

The Y chromosome of *O. canaliculata* may also be regarded as a deficiency chromosome, but it differs from the Y of *S. douthitti* in having a short differential segment, the heterochromatic right arm. Since the differential segment of Y is short and heterochromatic, whereas that of X is long and euchromatic, it seems likely that sex in this species is also determined by some mechanism other than that of a strongly female-determining Y.

Although *S. mansoni* lacks heteromorphic sex chromosomes which can be detected at mitosis, chromosome pair number 1, corresponding to the sex chromosomes of *S. douthitti* and *O. canaliculata*, is composed at pachytene of two identical euchromatic chromosomes in males, and of one euchromatic and one partially heterochromatic chromosome in females. The conclusion seems justified that the chromosome with the heterochromatic segment is, in fact, a Y chromosome, and that females of *S. mansoni* are therefore heterogametic. Female heterogamety in *S. mansoni* has been suggested earlier by the work of Vogel[13], who obtained matroclinal (presumably parthenogenetic) progeny composed of both sexes in crosses of *S. mansoni* females with *S. japonicum* males.

Evidence for female heterogamety in three genera of the Schistosomatidae suggests that this mechanism may prevail throughout the family. In all three species the X chromosome is the longest metacentric element. Such a chromosome is conspicuously present in the karyotypes of all of the nine species in six genera for which the mitotic chromosomes are known. We have previously inferred[12] that the ancestral schistosome stock possessed a genome of eight chromosomes, of which the longest (chromosome 1) was metacentric. It may now be suggested that this chromosome probably bore the original factors which gave rise to separate sexes in a previously hermaphroditic stock. Consideration of the relative positions of the differential and homologous segments of X and Y in the three species studied at pachytene (Figure 3*M*) suggests that the original sex-determining factors were located in the interstitial region of the right arm of chromosome 1.

The X chromosomes of the various species may well have remained rather similar during subsequent evolution. The Y chromosomes, on the other hand, apparently evolved from the ancestral X in various ways. In *S. mansoni*, Y has lost little or none of its original length, but the differential region has become somewhat heterochromatic, a feature which perhaps prevents crossing-over in this region. The Y of *O. canaliculata* may represent a more advanced (though not necessarily consecutive) stage of differentiation. Most of the right arm has been lost and what remains of it has become heterochromatic.

It is difficult to fit the Y of *S. douthitti* into a sequence with the Y's of *S. mansoni* and *O. canaliculata*, partly because the position of its centromere is uncertain. Its synaptic behavior makes clear, however, that it has lost a large part of the proximal regions of both arms, so that only the euchromatic regions corresponding to the ends of X remain.

Since the Y chromosomes of *S. mansoni* and *O. canaliculata* are only slightly heterochromatic as compared with those of most other species of animals, it is possible to determine the synaptic relations between the heterochromatic regions and the corresponding euchromatic regions of X. In most pachytene nuclei of both species, synapsis is as intimate in these regions as elsewhere despite the difference in chromaticity. If X and Y have both evolved from a primitive chromosome 1, either heterochromatinization has not conferred non-homology, or non-homology has not interfered seriously with synapsis.

Pachytene complements are known in only three of the more than 70 species and 12 or more genera of the Schistosomatidae. The present study suggests that similar studies of additional species would provide interesting clues both to the evolution of the sex chromosomes and to the relationships within the family.

Summary

Pachytene idiograms are presented for males and females of *Schistosomatium douthitti*, *Ornithobilharzia canaliculata*, and *Schistosoma mansoni*. Although the heteromorphic sex chromosome pairs of *S. douthitti* and *O. canaliculata* are similar in morphology at mitosis, their pachytene configurations show that they differ in the arrangement of pairing and differential segments. *S. mansoni* lacks a heteromorphic pair of sex chromosomes at mitosis, but at pachytene in females the longest bivalent, corresponding to the XY pair of the other two species, is composed of one euchromatic and one partially heterochromatic chromosome. Since in males the corresponding bivalent is composed of two euchromatic chromosomes, it is concluded that the partially heterochromatic chromosome is a Y and that females of *S. mansoni* are heterogametic, as are those of the other two species.

Literature Cited

1. Conger, A. D. and L. M. Fairchild. A quick-freeze method for making smear slides permanent. *Stain Tech.* 28:281-283. 1953.

2. Faust, E. C. and H. E. Meleney. Studies on schistosomiasis japonica. *Am. Jour. Hyg.* Monogr. Ser. 3, 339 pp. 1924.

3. Gray, Peter. The Microtomist's For-

mulary and Guide. The Blakiston Co., New York. 794 pp. 1954.

4. IKEDA, K. and S. MAKINO. Studies on the sex and chromosomes of the oriental human blood fluke, *Schistosomum japonicum* Katsurada. *Jour. Fac. Sci.*, Hokkaido Imp. Univ., 5:57-71. 1936.

5. LINDNER, E. Ueber die Spermatogenese von *Schistosomum haematobium* Bilh. (*Bilharzia haematobia* Cobb) mit besonderer Berücksichtigung der Geschlechtschromosomen. *Arch. Zellforsch.* 12:516-538. 1914.

6. MENZEL, M. Y. and R. B. SHORT. Unexpected pachytene behavior in *Schistomatium douthitti* (Abstract). *A.S.B. Bull.* 4:14. 1957.

7. NEZ, MARTHA M. and R. B. SHORT. Gametogenesis in *Schistosomatium douthitti* (Cort) (Schistosomatidae: Trematoda). *Jour. Parasitol.* 43:167-182. 1957.

8. NIYAMASENA, S. G. Chromosomen und Geschlecht bei *Bilharzia mansoni*. *Zeit. Parasitenk.* 11:690-701. 1940.

9. SEVERINGHAUS, A. E. Sex studies on *Schistosoma japonicum*. *Quart. Jour. Micro. Sci.* 71:653-702. 1928.

10. SHORT, R. B. Chromosomes and sex in *Schistosomatium douthitti*. Trematoda: Schistosomatidae. *Jour. Hered.* 48:2-6. 1957.

11. ———— and M. Y. MENZEL. Chromosomes in parthenogenetic miracidia and embryonic cercariae of *Schistosomatium douthitti*. *Exper. Parasitol.* 8:249-264. 1959.

12. ————. Chromosomes of nine species of schistosomes. *Jour. Parasitol.* 46:273-287. 1960.

13. VOGEL, H. Ueber die Nachkommenschaft aus Kreuzpaarungen zwischen *Bilharzia mansoni* und *B. japonica*. *Zentralbl. Bakteriol.* 1. Abt., Orig., 149:319-333. 1942.

In and Out of the Ivory Tower

ANY book about the life of Richard Goldschmidt* could not help but be fascinating. Not many have happened to be in the category of enemy alien during both World Wars. Few have seen so much of the world and none, of course, ever had quite the same panorama of experiences as Goldschmidt.

Naturally the autobiography begins with the neonatal and genealogical account. The baby was born with a silver spoon in his mouth and never took it out, except at rare intervals. The elegant German schools he attended are made to sound like something out of Dickens. He was obviously delinquency prone and had he behaved in Minnesota now, as he did in Frankfurt then, he would have been arrested and have qualified as a legitimate member of our army of juvenile delinquents. Fortunately, he discovered biology and gave up bedeviling his teachers and parents. Actually the problems of his youth were mostly those of the gifted child who is unemployed.

One tends to forget that Goldschmidt, like the other founders of genetics, had a well established scientific reputation before he turned to the new look at heredity. All geneticists are acquainted with Goldschmidt's work on the gypsy moth and its intersexuality. The reviewer could never develop much interest in this work, probably because he was influenced by the common prejudices that the world would be better off without either intersexuality or gypsy moths.

It was on the return trip from Japan and gypsy moth collecting that Goldschmidt found himself stranded in the United States at the outbreak of the first World War. His account of this experience is a little baffling. He was requested to do his gypsy moth work at the Bussey Institution, as this area was already swarming with the pests. If some of his Japanese moths escaped they could be no worse than those that had been introduced earlier. When the reviewer first went to the Bussey in 1930, there were still tales abroad of Goldschmidt's vigorous defense of the fatherland 15 years before. There is no hint in the book that Goldschmidt might have contributed in some small degree to his own difficulties, then. He does acknowledge that several Americans risked endangering themselves seriously in his behalf.

Goldschmidt was in the United States in 1932 for the International Genetics Congress at Ithaca. One morning the reviewer was having breakfast alone on the lovely terrace of Willard Straight Hall when he was joined by the great man. The reviewer mentioned his dismay at the favorable attention Hitler was receiving in Germany. Goldschmidt did not defend Hitler nor condemn him. He pointed out with vehemence what an insult it was to him to have to use a passport to visit East Prussia because the Polish Corridor stood in the way. He had nothing good to say for the

(*Continued on page* 18)

**In and Out of the Ivory Tower*. The autobiography of Richard B. Goldschmidt. 352 pp. University of Washington Press. 1960. $5.75.

MALE STERILITY IN INTERSPECIFIC HYBRIDS OF SOLANUM

RAYMOND W. BUCK, JR.*

DURING hybridization and cytological investigation of tuber-bearing *Solanum* species and hybrids, the author observed a type of male sterility, as expressed by pollen abortion, in F_1 hybrids involving certain clones of *S. verrucosum* Schlecht. *S. verrucosum*, a diploid species indigenous to Mexico, is one of the diploid species in the Section Tuberarium of the genus *Solanum* which are self-compatible. Most diploid species in Section Tuberarium are self-incompatible. Self-incompatibility of the diploid species is generally considered to be due to a series of simple oppositional alleles[3]. However, in certain crosses the mechanism controlling self-incompatibility appears more complex[1].

Crosses between *S. verrucosum* and diploid species from South America produce seed when *S. verrucosum* is the female parent. Most reciprocal crosses fail. However, the author succeeded in obtaining reciprocal hybrids with one clone of *S. phureja* Juz. & Buk. and with one clone of *S. chacoense* Bitt.

Pollen sterility was determined by staining pollen with aceto-carmine. Among the male-sterile plants, plants with as much as 45 to 50 percent stainable pollen occurred. However, the pollen grains from these plants showed evidence of breakdown of cytoplasm and stained very lightly as compared with deeply-stained grains from male-fertile plants.

Meiosis in both male-sterile and male-fertile plants is normal.

Results and Discussion

Male sterility occurs in all 11 interspecific hybrids with *S. verrucosum* P.I. 195171 and *S. verrucosum* P.I. 195172 as the female parent, (Table I). The four hybrids with *S. verrucosum* P.I. 161173 as the female parent are male-fertile, (Table I). Hybrids from the two successful reciprocal crosses, *S. chacoense* × *S. verrucosum* 195172 and *S. phureja* × *S. verrucosum* 195172, are also male-fertile, (Table I).

The male sterility of the hybrids *S. verrucosum* 195172 × *S. chacoense* and *S. verrucosum* 195172 × *S. phureja* and the male fertility of the reciprocal hybrids indicate that male sterility is determined by the cytoplasm of *S.*

TABLE I. Occurrence of male sterility in diploid hybrids of *Solanum*

Parentage			Number of plants	
			Male-sterile	Male-fertile
S. verrucosum P.I. 195171	×	*S. chacoense*	4	0
"	×	*S. macolae*	4	0
"	×	*S. phureja*	4	0
"	×	*S. phureja* P.I. 195191	4	0
"	×	*S. simplicifolium*	4	0
"	×	*S. stenotomum*	4	0
"	×	*S. toralapanum*	4	0
S. verrucosum P.I. 195172	×	*S. chacoense*	4	0
"	×	*S. macolae*	4	0
"	×	*S. phureja* P.I. 195191	2	0
"	×	*S. simplicifolium*	4	0
S. verrucosum P.I. 161173	×	*S. macolae*	0	4
"	×	*S. phureja*	0	4
"	×	*S. simplicifolium*	0	4
"	×	*S. tarijense*	0	4
S. chacoense	×	*S. verrucosum* P.I. 195172	0	13
S. phureja P.I. 195191	×	*S.* "	0	10

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verrucosum. The normal-appearing pollen of hybrids with *S. verrucosum* 161173 as the female parent indicates that a normal-type cytoplasm exists in this clone.

The backcrosses of four male-sterile hybrids to *S. verrucosum*, (Table II), segregate into male-sterile and male-fertile plants. All plants in the backcrosses of six male-sterile hybrids to the self-incompatible parent, (Table II), are male-sterile. F_2 progenies obtained by sibmatings of the male-fertile hybrids *S. chacoense* × *S. verrucosum* and *S. phureja* × *S. verrucosum* were male-fertile, (Table II).

The data, (Table II), indicate that male sterility is also controlled by a gene from the self-incompatible parent of the original crosses. Assuming that male sterility of the F_1 hybrids results from the interaction of a gene from the self-incompatible parent and the cytoplasm from *S. verrucosum*, a ratio of 1 male-sterile plant : 1 male-fertile plant would be expected in the backcrosses to *S. verrucosum*. Also the backcrosses to the self-incompatible parent should contain only male-sterile plants. The data, (Table II), indicate the correctness of this assumption. Forty plants in the backcrosses to *S. verrucosum* segregated into 22 male-sterile plants and 18 male-fertile plants. This fits the expected ratio of 1:1 with a chi-square of 0.40. Sixty plants in the backcrosses to the self-incompatible parent were all male-sterile. Possibly, genes controlling self-incompatibility from the self-incompatible diploid species in the presence of cytoplasm from *S. verrucosum* may determine male sterility in the hybrids. However, the exact identification of the gene is not possible from the data available.

East[2] found that plants derived from the cross *Nicotiana langsdorffii* × *N. sanderae* are male-sterile when they carry two *S* factors (self-incompatibility factors) from *N. sanderae* in the presence of cytoplasm from the self-compatible *N. langsdorffii*. Plants produced normal pollen and were self-incompatible when the *S* factors were in the presence of cytoplasm derived from *N. sanderae*.

The male sterility in *Solanum* is somewhat similar to that in *Nicotiana*. In both, the male-sterile cytoplasm is present in the self-compatible species and the gene is present in the self-incompatible species. However, there are two differences. Firstly, the F_1 hybrids are male-sterile in *Solanum*, but male-fertile in *Nicotiana*. Secondly, two genes are necessary to produce male sterility in the *Nicotiana* hybrids, whereas only one is necessary in the *Solanum* hybrids.

Summary

Male sterility, as expressed by pollen abortion, occurred in F_1 hybrids between the self-compatible species *S. verrucosum* and six self-incompatible *Solanum* species. The male sterility in these hybrids results from the interaction between the cytoplasm of *S. verrucosum* and a gene from the self-incompatible species. Two types of cytoplasm, one producing plants with aborted pollen and the second producing plants with normal pollen, are present within the species *S. verrucosum*.

Literature Cited

1. Carson, G. P. and H. W. Howard. Self-incompatibility in certain diploid potato species. *Nature* 150:290. 1942.

2. East, E. M. Studies on self-sterility. IX. The behavior of crosses between self-sterile and self-fertile plants. *Genetics* 17:175-202. 1932.

3. Pal, B. P. and Pushkarnath. Genetic nature of self- and cross-incompatibility in potatoes. *Nature* 149:246-247. 1942.

TABLE II. Segregation of male sterility in F_2 and backcrosses of *Solanum* hybrids

Parentage		Number of plants	
		Male-sterile	Male-fertile
Backcrosses of male-sterile hybrids to *S. verrucosum*:			
(*S. verrucosum* P.I. 195171 × *S. chacoense*) × *S. verrucosum*		4	6
(*S. verrucosum* P.I. 195171 × *S. phureja*) × "		5	5
(*S. verrucosum* P.I. 195171 × *S. stenotomum*) × "		7	3
(*S. verrucosum* P.I. 195172 × *S. chacoense*) × "		6	4
	Total	22	18
Backcrosses of male-sterile hybrids to self-incompatible parent:			
(*S. verrucosum* P.I. 195171 × *S. chacoense*) × *S. chacoense*		10	0
(*S. verrucosum* P.I. 195171 × *S. macolae*) × *S. macolae*		10	0
(*S. verrucosum* P.I. 195171 × *S. phureja*) × *S. phureja*		10	0
(*S. verrucosum* P.I. 195171 × *S. simplicifolium*) × *S. simplicifolium*		10	0
(*S. verrucosum* P.I. 195172 × *S. chacoense*) × *S. chacoense*		10	0
(*S. verrucosum* P.I. 195172 × *S. simplicifolium*) × *S. simplicifolium*		10	0
	Total	60	0
F_2 hybrids:			
F_2 (*S. phureja* P.I. 195191 × *S. verrucosum* P.I. 195172)		0	22
F_2 (*S. chacoense* × ")		0	32
	Total	0	54

FURTHER STUDIES ON THE INHERITANCE OF LOOSE PERICARP IN CORN

G. A. LEBEDEFF*

IN a previous report[1] loose pericarp in corn was described for the first time. In kernels with loose pericarp the endosperm fills about three-quarters of the kernel space, making the pericarp loose at the tip. Inheritance of this character was studied in crosses between two inbred lines, Mpl and GE54. Ears of Mpl have a well pronounced loose pericarp, and ears of GE54 are smooth except for prominent silk scars which make them prickly to the touch. This study indicated that loose pericarp is inherited as a quantitative character.

The present paper deals with the inheritance of loose pericarp in crosses between inbred line Mpl and the Flint variety, and between Mpl and two other inbred lines, Tx203 and GE129, which have ears with loose pericarp. These studies were conducted in 1958 and 1959; however, some of the material was grown in previous years. The ears of inbred lines and those of progenies from various crosses were classified according to six pericarp grades, as in the previous study[1]. The grades ranged from smooth through various degrees of roughness to loose pericarps. Some ears of the middle grades of pericarp were not as rough as those of progenies in the previous study. The smaller size and harder kernels of some of the material in the present study as well as seasonal influence may contribute to this effect.

Experimental Results

Crosses between inbred Mpl and the Flint variety

The results of the Mpl-Flint cross are given in Table I. The ears of the F_1 progeny showed a pronounced skewed distribution with a mean pericarp grade of 1.20. This value is close to that of the ears of the Flint variety, and it is considerably lower than the mid-parent value of 3.45, (Table I, rows 1-3). The ears of the F_2 progeny also showed a skewed distribution for pericarp grades with a mean of 1.49, but with a greater spread in grades than in the F_1.

There were 20 F_3 progenies of the Mpl-Flint cross available. The F_2 parent ears of these progenies were of grades 1 and 2, and there was good agreement between classification of F_2 and F_3 ears. The eight progenies of the grade 1 parents were grouped together, as were 12 progenies of the grade 2 parents. Their respective means for pericarp grades were 1.59 and 1.86, (Table I, rows 5 and 6). These results indicate that

TABLE I. Frequency distribution for pericarp grades in Flint variety, Mp1 inbred line, and F_1, F_2, F_3 and backcrosses of Mp1-Flint cross

Row	Inbred or Cross	Progeny pericarp grades 1	2	3	4	5	6	Total	Mean
1	Flint variety	83						83	1.00
2	Mpl					15	153	168	5.91
3	(Mpl × Flint)F_1	163	19	10				192	1.20
4	(Mpl × Flint)F_2	660	358	68	12	3		1101	1.49
5	(Mpl × Flint)F_3*	175	170	19	3			367	1.59
6	(Mpl × Flint)F_3**	191	398	59	1	13		662	1.86
7	(Mpl × Flint)×Flint	1413	24	2				1439	1.02
8	(Mpl × Flint)×Mpl	69	237	171	119	20	1	617	2.65

*Summary of eight F_3 progenies whose F_2 parent had grade 1 pericarp.
**Summary of 12 F_3 progenies whose F_2 parent had grade 2 pericarp.

*Georgia Experiment Station, Experiment, Georgia. Paper No. 370, Journal Series.

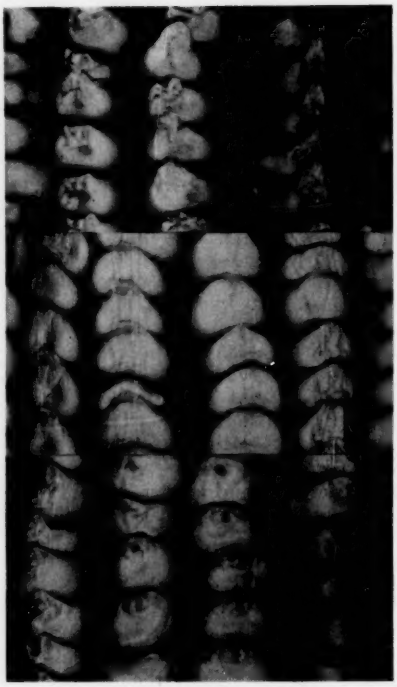
smooth pericarp is dominant over loose pericarp in the Mpl-Flint cross. There is indication that three major genes are involved. If the ears of grades 1 through 3 and of grades 4 through 6 are grouped together, there is a 1086:15 ratio of "smooth" vs. "loose" grades of pericarp, which approximates a 63:1 ratio, (Table I, row 4). The results of backcrosses support a hypothesis of smooth pericarp dominance. The mean pericarp grade of (Mpl × Flint) × Flint progeny was 1.02, similar to that of the Flint parent. The mean pericarp grade of (Mpl × Flint) × Mpl progeny was 2.65, which is a deviation in the plus direction of 1.45 in grade from the F_1 mean, (Table I, rows 7 and 8).

Crosses between inbred lines with loose pericarp

Loose pericarp appears to be not uncommon, although it has not been recognized previously. Since these studies were initiated, several inbred lines with loose pericarp have been identified, and two of these lines, Tx203 and GE129, have been studied. Both of these lines, as well as Mpl, have been inbred for many generations and may be considered homozygous lines.

Ears of Tx203 have a pronounced loose pericarp approaching that of Mpl. Loose pericarp in GE129 ears is not as pronounced, (Figure 5). Kernels of Tx203 and GE129 were dissected in the milk stage, and looseness of the pericarp was evident in both of these inbred lines, but more so in Tx203 than in GE-129. For examination for loose pericarp, kernels in the milk stage before indentation of the endosperm develops were found to be satisfactory.

The results of the Tx203-Mpl cross are summarized in Table II. The F_1 progeny had ears with loose pericarp identical with those of the Tx203 parent, mean grades of pericarp being 5.21 and 5.23, respectively, (Table II, rows 1-3). The pericarp grade of the F_2 progeny was 5.09, a value only slightly below that of the F_1 progeny, but in the F_2 there were segregates for the smoother pericarp grades 1, 2 and 3 which are not found in progenies of either parent, (Table II, row 4). These results indicate that loose pericarp of Tx203 and Mpl is



LOOSE PERICARP OF INBRED LINES

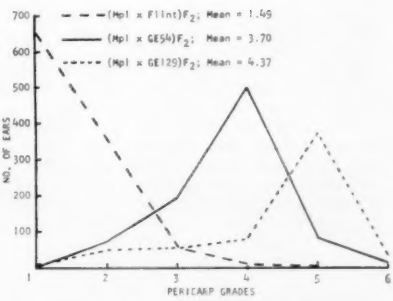
Figure 5

Small portions of ears of corn are shown approximately twice natural size. *A*—Mpl: *B*—Tx203; *C*—GE129.

TABLE II. Frequency distribution for pericarp grades of Tx203, Mpl inbred lines, and F_1 and F_2 of Tx203-Mpl cross

Row	Inbred or Cross	Progeny pericarp grades 1	2	3	4	5	6	Total	Mean
1	Tx203					51	15	66	5.23
2	Mpl					15	153	168	5.91
3	(Tx203 × Mpl)F_1					140	41	181	5.21
4	(Tx203 × Mpl)F_2	5	13	20	49	243	197	527	5.09

not alike genetically. The results of the GE129-Mpl cross are given in Table III. The mean pericarp grade of the F_2 progeny was 4.37, a value considerably lower than that for either parent. The appearance of the smoother pericarp grades 1, 2 and 3 in considerable numbers in the F_2 indicates that inbreds GE129 and Mpl also differ genetically. Comparing the results of the Tx203-Mpl and the GE129-Mpl crosses, it is evident that inbred lines Mpl, Tx203, and GE-129 have major genes in common for loose pericarp, but differ from each other in minor or modifying genes. Some of the minor genes are dominant, which is manifested in the appearance of smooth grades of pericarp in F_2 of Tx203-Mpl and GE129-Mpl crosses. This indicates genetic diversity of inbred lines.



F_2 FREQUENCY DISTRIBUTION FOR PERICARP GRADES

Figure 6

Frequency curves for pericarp grades of the F_2 progenies from Mpl-Flint, Mpl-GE54 and Mpl-GE129 crosses are shown above.

Discussion

To evaluate the genetic system by which the loose pericarp is controlled, frequency curves for pericarp grades of the F_2 progenies from Mpl-Flint, Mpl-GE54[1], and Mpl-GE129 crosses are presented in Figure 6. The progeny from the Mpl-Flint cross shows a pronounced skewed distribution, indicating that the smooth pericarp of the Flint variety is dominant over loose pericarp. The F_2 results from the Mpl-GE54 cross shows a unimodal frequency curve which is skewed toward smooth grades of pericarp. This indicates that the genes for pericarp grades of the GE54 parent have some degree of dominance over loose pericarp. The F_2 progenies from Mpl-GE129 and Mpl-Tx203 crosses also show unimodal frequency distributions for pericarp grades. However, these progenies segregate for pericarp grades which are considerably smoother than those of either parent. This indicates dominance of loose pericarp over smooth grades of pericarp in Mpl-GE129 and Mpl-Tx203 crosses.

According to a generally accepted hypothesis dent corn resulted from crosses of Flint varieties with the Gourdseed variety[2]. Flint kernels are small, shallow and hard, as they contain very little soft starch, and are smooth in appearance. Gourdseed kernels are large and rough and contain a large amount of soft starch. Dent corn has a depression in the crown of the kernel, which is caused by unequal shrinkage of hard and soft starches. The relative positions and the amounts of soft and hard endosperm produce differences in the character and extent of indentation, which may vary from a mere dimple to a ragged dent or projecting flap.

In view of our study on loose pericarp it would be desirable to project the possible effect of pericarp on denting. The difference in size of kernel, and hence of the pericarp, in the Flint and Gourdseed varieties is considerable. In Flint corn the pericarp is tight, while in the Gourdseed variety the pericarp appears to be too large for the content of the kernel. When such extreme types are crossed, great variations in size of pericarp in relation to the content of kernels may be found in succeeding generations. The rough types of dent corns, often with "projecting flaps," may be the result of a loose pericarp.

Summary

Inheritance of loose pericarp was studied in crosses between inbred line Mpl and the Flint variety, and between Mpl and two other inbred

TABLE III. Frequency distribution for pericarp grades of GE129, Mp1 inbred lines, and F_1 and F_2 of GE129-Mp1 cross

Row	Inbred or Cross	Progeny pericarp grades 1	2	3	4	5	6	Total	Mean
1	GE129			4	6	77	1	88	4.85
2	Mpl					15	153	168	5.91
3	(GE129 × Mpl)F_1*				20	72		92	4.78
4	(GE129 × Mpl)F_2	16	53	57	81	376	32	615	4.37

*Classification of this progeny is uncertain.

lines, Tx203 and GE129, which have ears with loose pericarp.

Smooth pericarp of Flint corn is dominant over loose pericarp of Mpl. There is an indication that three major genes are involved in differentiating these grades of pericarp.

The results of Tx203-Mpl and GE129-Mpl crosses indicate that although these three inbred lines have loose pericarp, they differ genetically. The appearance of smooth grades of pericarp in F_2 of these crosses indicates that these inbreds carry some modifying genes dominant over those of smoother grades of pericarp.

A possible relationship between loose pericarp and denting in corn is suggested.

Literature Cited

1. LEBEDEFF, G. A. Inheritance of loose pericarp in corn. *Jour. Hered.* 49:128-131. 1958.

3. WALLACE, HENRY A. and E. N. BRESSMAN. Corn and Corn Growing. John Wiley & Sons, Inc., N. Y. 437 pp. 1937.

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In and Out of the Ivory Tower

(*Continued from page* 12)

Polish Jews who had come to Germany and bought land at bargain prices when the mark was dropping in value every hour. The conversation shocked me, as I had expected vigorous rejection of everything related to the Nazi program, which was well known though not yet in force. If Germany's old wounds hurt Goldschmidt this much, it is easy to see how Hitler came to power supported by those who thought they had nothing to lose.

In 1933 Goldschmidt began to be a little uneasy about the situation. He came to the United States in 1936 and legally in 1941 became an enemy alien again—but this time he did not defend Germany. His main humiliation was that of having to teach undergraduates at the University of California. He says he found the work most hateful and felt rather déclassé. So much for Goldschmidt's problems.

The other side of the coin is Goldschmidt's pleasures. These occupy most of the book and the reader will enjoy them as much as Goldschmidt did. He knows how to write! You will climb the mountains and bask in the tropics with him. It is easy to share his love for music and paintings. A photograph in the book gives a good idea of his superlative collection of Chinese tomb figurines when on exhibit in the San Francisco Museum. These treasures of his life will be shared by all who will read the pages of this enthralling story. It is difficult to tear yourself away from the book. Who would want to give up his trip around the world before it is finished? Everyone will want to stay with the hero until he gets out of the Hartford city jail.

Autobiographies of geneticists are exceedingly rare. What motivated this one, in which there is no particular attempt to justify any scientific theories? The reviewer's guess is that Goldschmidt loved to write as an artistic experience. It gave him the same satisfaction as playing the violin. His own life provided the richest and most exciting subject material he could find. The combination of a superb true story and exceptional writing skill results in a book which anyone should be able to enjoy intensely. The general public will be surprised to find that a scientist whose main concern for years was intersexuality in the gypsy moth was intensely human and lived dangerously!

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INDUCED SUBCHROMOSOME BREAKS IN PROPHASE OF VICIA FABA

IRVING GALINSKY*

THE treatment of *Vicia faba* with various substances has been reported to induce chromosome breaks[3, 4, 7, 8, 9]. The type of breakage is generally inferred from the chromosome configurations observed at metaphase and anaphase. While it has been suggested that chromatid and subchromatid breaks occur at prophase[6] or just prior to it[5], there has been difficulty in observing this phenomenon directly on prophase chromosomes. The reason for this is the difficulty of obtaining mitotic prophase chromosomes which are well-spread, in which the chromatids are adequately separated, and which also contain breaks.

The following is a report of an exceptionally well-spread, early mitotic prophase of *Vicia faba* in which chromatid and subchromatid breaks have been induced by treatment with disodium phosphate.

Materials and Methods

Seeds of *Vicia faba* were germinated in a dish containing water-soaked filter paper. When the roots were about two cm. long, they were immersed in a 0.025M solution of disodium phosphate for six hours at room temperature. The roots were then fixed in Carnoy, stained with Feulgen, and smeared.

Results and Discussion

The usual manifestations of chromosome breaks were seen at metaphase and anaphase but attempts to observe breaks in the prophase chromosomes were not very successful. However, one exceptionally well-spread, early prophase was obtained where chromatid and half-chromatid breaks could readily be seen. The prophase chromosomes shown in Figure 7 consist of two chromatids and each chromatid contains two spiralled chromonemata or half-chromatids. Chromatid breaks are shown by the arrows at 1, 3, and 6, and a half-chromatid break at 2. The large chromosome at the bottom center has a peculiar type of configuration. The two chromatids are well separated at the bottom and there appears to be an extra chromatid attached to each arm. Each of these attached chromatids contains a break (arrows 4 and 5) and the chromonema of the half-chromatids can readily be seen.

PROPHASE CHROMOSOME BREAKS

Figure 7

Chromatid and subchromatid breaks in prophase chromosomes of *Vicia faba* treated with disodium phosphate. ×2000.

The occurrence of breakage in the subunits of the chromosome had been reported by others from metaphase and anaphase configurations. La Cour and Rutishauser[6] concluded that the

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anaphase configurations in X-rayed endosperm resulted from subchromatid breakage during prophase. Bird and Fahmy[1] treated *Drosophila* sperm with diepoxybutane and found damaged subchromatids in the salivary gland chromosomes. Kihlman and Levan[5] used ethoxycaffeine and found chromatid breaks in roots of *Vicia faba*. They concluded that as a rule the chromosome breaks occurred on the same level in both chromatids. Their observations differ from those on the disodium phosphate-treated *Vicia* prophase in Figure 7 where only chromatid and subchromatid breaks are evident and these are not on the same level of the chromosome.

It is possible that an appropriate concentration of inorganic phosphate interferes with some process necessary for the complete duplication of parts of the chromonemata. Certain concentrations of inorganic phosphate have been reported to inhibit such enzymes as glucose-6-phosphate dehydrogenase, phosphoglucose isomerase, adenylic deaminase, purine nucleosidases, xanthine oxidase, and phosphatase[9]. The high proportion of chromatid and subchromatid breaks observed suggests that these may be due to an interference in the synthesis of a portion of the chromonema.

Summary

Treatment of *Vicia faba* roots with a solution of disodium phosphate resulted in breaks in the subunits of the chromosomes. These were very difficult to detect in early mitotic prophase but an exceptionally well-spread early prophase revealed chromatid and subchromatid breaks.

Literature Cited

1. Bird, M. J. and O. G. Fahmy. Cytogenetic analysis of the action of carcinogens and tumor inhibitors in *Drosophila melanogaster*. I. 1:2, 3:4-diepoxybutane. *Proc. Roy. Soc. London* B140: 556-578. 1953.

2. Colowick, S. P. and N. O. Kaplan. Methods in Enzymology. Vols. I and II. Academic Press, Inc., N. Y. 1955.

3. Darlington, C. D. and J. McLeish. Action of maleic hydrazide on the cell. *Nature* 167:407-408. 1951.

4. Ford, C. E. Chromosome breakage in nitrogen mustard treated *Vicia faba* root tip cells. *Proc. Eighth Int. Cong. of Gen.* (*Hereditas*, Suppl. Vol.): 570-571. 1949.

5. Kihlman, B. and A. Levan. Localized chromosome breakage in *Vicia faba*. *Hereditas* 37:382-388. 1951.

6. La Cour, L. F. and A. Rutishauser. Chromosome breakage experiments with endosperm: sub-chromatid breakage. *Nature* 172: 501-502. 1953.

7. Levan, A. and T. Lofty. Spontaneous chromosome fragmentation in seedlings of *Vicia faba*. *Hereditas* 36:470-482. 1950.

8. Loveless, A. and S. Revell. New evidence on the mode of action of mitotic poisons. *Nature* 164:938-944. 1949.

9. Swanson, C. P. and J. Merz. Factors influencing the effect of B-propriolactone on chromosomes of *Vicia faba*. *Science* 129:1364-1365. 1959.

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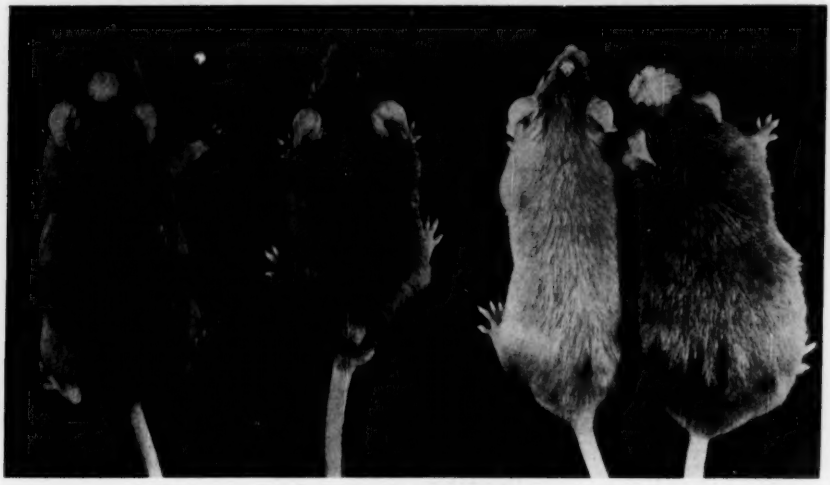
National Science Foundation Research Proposals

The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of basic research proposals in the Life Sciences is September 15, 1960. Proposals received prior to that date will be reviewed at the fall meetings of the Foundation's advisory panels and disposition will be made approximately four months following the closing date. Proposals received after the September 15, 1960, closing date will be reviewed following the spring closing date of January 15, 1961. Inquiries should be addressed to the National Science Foundation, Washington 25, D. C.

"DORSAL EXCRESCENCES" IN THE MOUSE—GENETIC OR NON-GENETIC?

ELIZABETH M. CENTER*



DORSAL EXCRESCENCES

Figure 8

Four mice showing dorsal excrescences. Nodular growths or accessory tufts of hair are found on the head or along the mid-dorsal line.

REPRESENTATIVES of a group of unusual traits which fall on the borderline between what is clearly hereditary and what is probably not so have appeared in our colony in the form of a number of manifestations which conveniently may be characterized as "dorsal excrescences." To group them all under one heading may be an oversimplification but it is not immediately apparent that such is actually the case. Prevailingly, they are characterized by nodular growths or accessory tufts of hair found on the head or at various points along the mid-dorsal line (Figure 8).

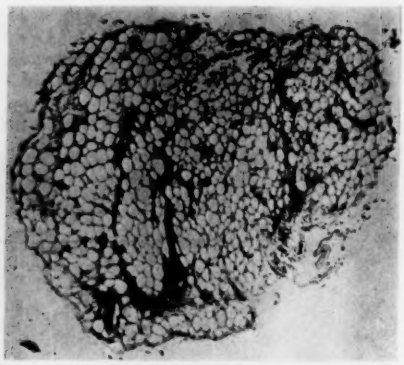
In the adult these anomalies often appear superficially as no more than specialized "tufts" of hair, but upon dissection a nodule or tissue mass of varying size is frequently found beneath the tuft. In the head region, the nodules are generally directly over or adjacent to a cranial suture, which occasionally shows abnormal development. They are also sometimes connected to the underlying meninges by a stalk which passes through a foramen. The condition can be recognized in the newborn, occasionally appearing in the form of a fluid-filled sac or, more often, as a spur-like tissue process. This is subsequently covered with hair, which in colored animals tends to be lighter than that of the surrounding region.

Cross sections of two such structures

*Department of Anatomy, Stanford University School of Medicine. This investigation was supported by a research grant (#1385) from the National Institutes of Health, Department of Health, Education and Welfare, administered by C. H. Danforth. The writer wishes to express appreciation for valuable assistance from members of the staff of the Department of Anatomy and to especially thank Dr. Danforth for his generous help and advice.

LUMBO-SACRAL APPENDAGE
Figure 9

Section through a lumbo-sacral excrescence showing an accessory spinal cord and accompanying ganglia in a 13-day embryo.



CRANIAL APPENDAGE
Figure 10

Section through the cranial excrescence of an adult mouse revealing for the most part only fatty and connective tissues.

(Figures 9 and 10) reveal that there may be little, or quite extensive, organization within them. These specimens serve to emphasize the morphological, and perhaps genetic diversity of the excrescenses. Figure 9 is a section through a lumbo-sacral appendage, and Figure 10 through a cranial one. The former includes an accessory partially organized spinal cord with accompanying ganglia, while the latter is predominantly fat and connective tissue with a few strands of striated muscle evident in the center.

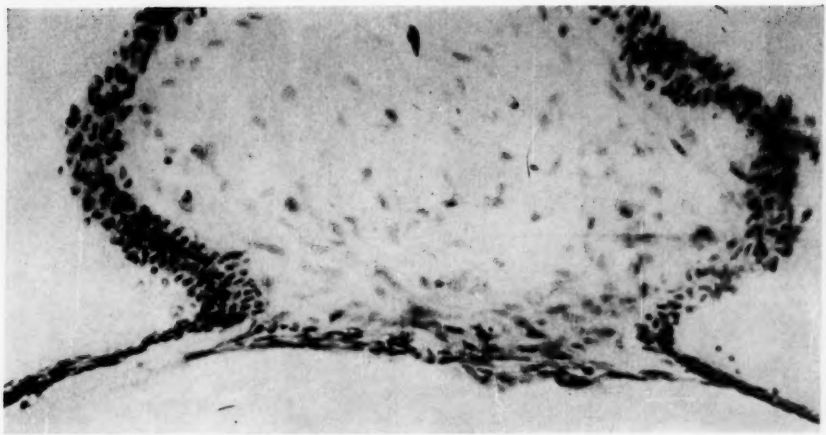
Examples of such manifestations, possibly representing induced mutations, have been found in several different stocks of mice whose ancestors were subjected to treatment with methyl bis (beta chloroethyl) amine hydrochloride (HN_2). These stocks included C57BL/6, two Stanford subgroups (S-br and a general purpose stock designated as "Stanford stock"), and various hybrid lines.

Taken as a group, the manifestations do appear in some cases to be hereditary, but not in any as yet clearly defined manner. A routine procedure has been to mate together whenever possible animals possessing some form of the characteristic. Unfortunately, data from such matings are limited due to the fact that suitable animals have not often coexisted in our colony. However, out of 84 offspring from these matings one showed an excrescence. This is obviously a very low incidence which might easily be attributed to chance.

As an alternative procedure animals possessing the trait were mated to sibs, parents or the closest available relatives and successive progenies backcrossed to the original variant animal for as many generations as feasible. When it was not possible to backcross to the individual showing the excrescence, inbreeding of closely related descendants or other relatives of this animal was continued.

One line was started by crossing a male showing a large cranial excrescence to possible sib females. Among the inbred descendants of this male, three mice were found to have a cranial or lumbo-sacral excrescence. In addition, among the inbred progeny of a male with a hair-bearing prominence on his nose, four animals showed either a cranial excrescence or a prominence on the nose. Two of these were found in the first generation backcross utilizing this male and two daughters resulting from matings to closely related females. All of the mice included in these two inbred groups were from the "Stanford stock."

However, the data sometimes fail to indicate that some characteristics which might be classified as dorsal excrescences



DORSAL EXCRESCENCE

Figure 11

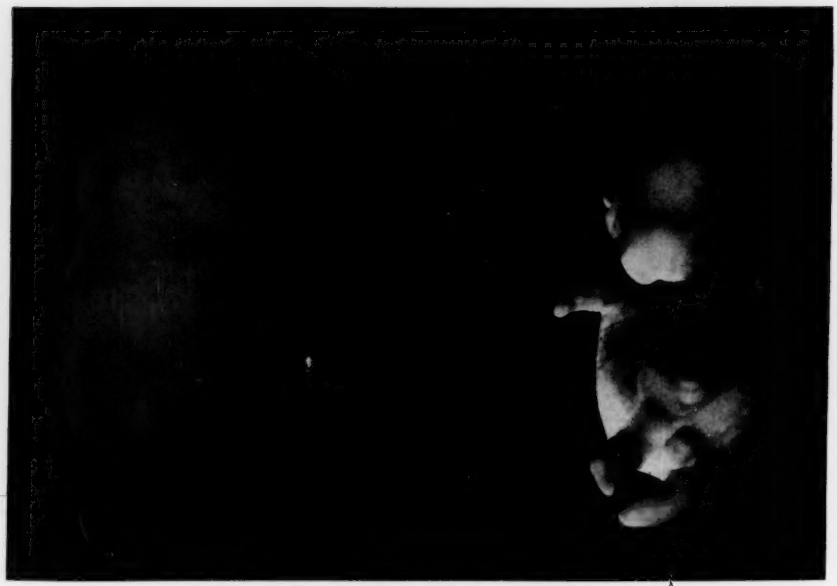
Section through a dorsal excrescence from a 14-day embryo in which there appears to be continuity between the excrescence and underlying intra-cranial tissues.

have any genetic basis whatever. For example, a male with a lumbo-sacral expression was mated to related females who were possibly his sibs or one of them his mother. Out of over 310 inbred young from these crosses none showed an excrescence, or anything morphologically similar. This abnormal animal was also a "Stanford stock" male. In an inbred strain, C57BL/6, four manifestations that could be placed in this group were noted in the 5,434 descendants from HN_2 treated animals, while no cases were found in the 1,116 descendants of the comparable C57BL/6 controls examined. This gives an over-all incidence of 0.06 percent in this group of C57BL/6 mice. Searle[9] recorded four cases of a "crest condition" (apparently the same as our cranial excrescences) in approximately 1,500 C57BL/Gr mice maintained in London, which would imply an incidence of 0.27 percent, about four and a half times as great as in the above mentioned group of C57 in our stock.

The highest recorded incidence in our colony was noted in a hybrid line. A male without an excrescence himself but from a "Stanford stock" subline with a somewhat sporadic incidence of anomalies of this type was crossed to a C3H female. In the latter stock no excrescences were noted in our laboratory nor, in so far as I have ascertained, in C3H stocks maintained elsewhere. Nevertheless, when two daughters from this mating were subsequently backcrossed to their father, a male with a sacral excrescence was found in the BC_1. This BC_1 male was then mated to another BC_1 female which lacked an excrescence and to his sib which also did not possess this characteristic. Out of the 160 examined progeny from these matings four animals with a cranial excrescence were found, giving a percentage incidence of 2.5, suggesting that this BC_1 male carried and transmitted one or more genetic factors favoring phenotypic expression of these "dorsal excrescences."

Possible sporadic manifestations in other hybrid groups of animals have also been recorded. Two such anomalies were found among 546 examined descendants from one hybrid female and one among 216 descendants of a C57 $\times$ S-br cross. Isolated cases were also observed in the F_1 progeny of a cross between Swiss and S-br and among the descendants of a C57 $\times$ Stanford subline mating.

If these excrescences can be interpreted as variable manifestations of a



EMBRYONIC CEREBRAL HERNIA

Figure 12

Fourteen-day embryos (treated three days prior with HN_2) showing cranial excrescences.

single genotype, the data would seem to indicate that some of them do have a hereditary background, although it is apparent that they do not follow any simple Mendelian pattern.

In morphology, at least some of them appear to have been initially masses of nervous tissue and surrounding meninges which, perhaps as the result of internal pressure, are forced outside their usual limits where they partially or sometimes completely lose their central connection and become degenerate.

A section of an embryo (approximately 14 days old) with a dorsal excrescence appears (Figure 11) to show continuity between the "crest" and underlying tissues within the cranium. It would seem that such cases differ both embryologically and morphologically from the type of hydrocephalus studied by Hertwig[5]. It might also be suspected that some of them represent failure of complete closure of the neural tube, but adequate and convincing evidence in favor of this idea is not available. It also seems that at least those in the cranial region are related to conditions ("parted frontals") studied by Keeler[6]. The more caudal expressions may be in some cases, such as the one shown in Figure 9, lesser expressions of, or somewhat related to, the phenomenon of "posterior duplication"[1]. Certain of the manifestations may have factors in common with the haemorrhagic lesions, subsequently referred to as "myencephalic blebs," first studied by Little and Bagg[8].

What appear to be manifestations morphologically parallel to the above-discussed variants have been induced by direct treatment of embryos with HN_2[2]. Animals with cranial excrescences in the form of "blisters" or apparent cerebral hernias (Figure 12) were noted subsequent to treatment on the tenth or eleventh day of intra-uterine life. On the basis of such observations it is conceivable that some of the cases which might be thought of as non-hereditary variants are

the result of a chance alteration in the intra-uterine environment by some specific agents which happened to become effective during gestation.

Discussion

These abnormalities are of interest largely because of the problems which they suggest. If they can be interpreted as different manifestations of a single underlying genotype, the problem arises as to why in certain stocks they appear to be non-hereditary variants and in others to be rather clearly hereditary. Searle[9] concluded that the appearance of the "crest condition" is dependent upon non-genetic factors within the C57 strain, but that "the ability to produce this variant depends on the genetic constitution" which is tantamount to saying that they are indeed hereditary. Goldschmidt[3] noted that without special investigation many mutants with low penetrance would be classified as non-hereditary variants. Thus, it seems that until clearly defined genetic factors can be demonstrated, the question of whether or not such traits as these are hereditary must remain in doubt.

The genetic behavior of dorsal excrescences is of interest in another respect. This is their apparent increased incidence in certain hybrid stocks, as if part of the necessary genetic factors were present in each parent and that these are brought together in the hybrid, thus making phenotypic expression possible. Or, conversely, one might suppose that each stock had independently developed suppressors whose effects are themselves abolished in the hybrids so that the variation can be expressed. Perhaps some clarification may be derived from Lerner's[7] concept of "genetic homeostasis" which is based in part upon the concept that natural selection favors intermediate phenotypes (i.e. hybrids) rather than extreme manifestations, and which implies that hereditary variants appear to be sporadic because of occasional suppression of factors which tend to maintain a state of genetic balance or homeostasis.

Goldschmidt and Piternick[4] noted in their study of chemically induced phenocopies that one of the possible explanations for the phenomenon which they studied may be "the presence or absence of subthreshold mutants at many loci, the action of which can be shifted above the threshold of visibility." One might suspect that such a system is in operation in the group of characteristics now under consideration, for intra-uterine treatment can apparently result in the production of phenocopies of the presumably genetic variants. One may perhaps assume that the generalized "genetic background" necessary for the expression of such anomalies may be at least in part "subthreshold mutants" which, responding about equally well either to internal genetic factors or to special external agents, result in phenotypically indistinguishable expressions. It would seem that in this area perhaps may be found some of the answers to questions that arise concerning variation in penetrance and expressivity noted for many traits.

Conclusions and Summary

A group of manifestations characterized by nodular tissue growths or accessory tufts of hair found on the head or at various points along the mid-dorsal line might be grouped together as "dorsal excrescences" and considered to be: (a) different expressions of one basic genotype, (b) manifestations of several different genetic entities, or (c) the result of factors some of which cannot be considered as strictly genetic. Morphologically, at least some of these excrescences appear to be masses of neural tissue or surrounding meninges which are forced outside the usual limits of the neural tube. Available data are sufficient only to indicate that in some instances there is an underlying genetic mechanism. An apparent increase of incidence in certain hybrid lines may reflect: (a) the bringing together in the hybrid of all genetic factors necessary for phenotypic expression, (b) a release in the hybrid from the effect of inhibitory genes, or (c) a disturbance of factors important in maintaining an underlying "genetic homeostasis."

Apparently morphologically parallel manifestations may result either from inherent genetic factors or from intra-uterine treatment. This suggests that possibly a matrix of predisposing and to some extent balanced genetic factors exist at a subthreshold level; treatment with an external agent or addition of new genetic elements adds what is necessary to bring the aggregate effect above the threshold which makes phenotypic expression possible.

It may be observed in conclusion that dorsal excrescences serve to emphasize a major difficulty frequently encountered in genetic analysis, especially in the complicated biological systems found in mammals. This is the problem of determining the basic factors involved in manifestations which appear to be morphologically and genetically related but which show a considerable range in phenotypic expression and a low, often seemingly sporadic, incidence. The problem is often dismissed as involving no more than "pleiotropism," "poor expressivity," or "low penetrance"; but such characterizations provide no real explanation and leave the nature of the underlying mechanisms still in doubt. The solution awaits the development of new or more adequate techniques for studying the factors underlying phenotypic expression of a complex biological system.

Literature Cited

1. Danforth, C. H. Developmental anomalies in a special strain of mice. *Amer. Jour. Anat.* 45:275-287. 1930.

2. ———— and E. M. Center. Nitrogen mustard as a teratogenic agent in the mouse.

Proc. Soc. Expr. Biol. & Med. 86:705-707. 1954.

3. Goldschmidt, Richard B. *Jour. Madras Univ.* B27, No. 1. Centenary Number: 17-24. 1957.

4. ———— and L. K. Piternick. The genetic background of chemically induced phenocopies in *Drosophila*. *Jour. Exp. Zool.* 135:127-202. 1957.

5. Hertwig, P. Untersuchungen uber die Taubheit bei einem Stramm von röntgen mutierten Mausen, den "syndactylen Schuttlern". *Proc. 8th Int. Congr. Genet.*: 592-593. 1948.

6. Keeler, C. E. Parted parietals in mice. A dominant hereditary character in the house mouse, *Mus musculus*. *Jour. Hered.* 21:19-20 and 83 (Page 83 corrects "parietals" to "frontals"). 1930.

7. Lerner, I. M. Genetic Homeostasis. John Wiley & Sons, Inc., New York, 1954.

8. Little, C. C. and H. J. Bagg. A brief description of abnormalities observed in the descendants of x-rayed mice. *Anat. Rec.* 24: 413-414 (Abstract). 1923.

9. Searle, A. G. 'Crest' in the house mouse. *Jour. Hered.* 44:173-176. 1953.

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THE TERATOLOGY SOCIETY

For several years scientists interested in basic problems of congenital malformations have held informal conferences in which questions of common interest were discussed. Anatomists, biochemists, embryologists, geneticists, obstetricians, pathologists, pediatricians, plastic surgeons and others attended these conferences which were in part supported by the Association for the Aid of Crippled Children, New York, N.Y., and the Human Embryology and Development Study Section of the National Institutes of Health. With the increased interest in recent years in this area, it was felt that there was a need for a Society to hold regular meetings in which investigations concerned with etiology and morphogenesis of congenital malformations could be presented and discussed. Following the fourth teratology conference, which was held at the Memorial Sloan-Kettering Cancer Center in New York City and attended by 76 scientists from Canada, England, France, Germany and the U.S.A., "The Teratology Society" was formed for the purposes outlined above. The following officers were elected: President: Josef Warkany, M.D., Cincinnati, Ohio; President-Elect: James G. Wilson, Ph.D., Gainesville, Fla.; Secretary-Treasurer: Marjorie M. Nelson, Ph.D., San Francisco, Calif.; Recorder: Sidney Q. Cohlan, M.D., New York, N.Y.; Council: F. Clarke Fraser, Ph.D., M.D., Montreal, Canada, David L. Gunberg, Ph.D., Portland, Ore., and M. Lois Murphy, M.D., New York, N. Y. The National Foundation assisted in the formation of the Society with advice and financial aid. Inquires about The Teratology Society should be directed to Dr. Marjorie M. Nelson, Department of Anatomy, School of Medicine, University of California, San Francisco 22, Calif.

MALE-STERILE FLOWER ANOMALIES IN INTERSPECIFIC TOBACCO HYBRIDS

L. G. BURK*

IN a study of two interspecific hybrids and their backcross generations, Clayton[1] observed that male-sterility plus modification of the stamens and corolla was associated with a displacement of the maternal genome by chromosomes of the recurrent parent in the presence of maternal cytoplasm. Koopmans[3] presented similar data and suggested that, in certain *Solanum species* hybrids, plasmatic influences control the development of abnormal flowers; i.e., that the genes of one *Solanum species* cannot function normally in the cytoplasm of another.

The writer has observed examples of flower anomalies in three interspecific *Nicotiana* hybrids. Derivatives of (*4n* (*N. bigelovii* × *N. tabacum*) × *N. tabacum*)BC^2 produce male-sterile plants according to the alien cytoplasm-chromosome interaction described by Clayton[1] and Koopmans[3]. However, two other male-steriles of the anomalous-flower type in which the cytoplasm of the F_1 hybrids originated from the recurrent backcross parent *N. tabacum* were noted. These were *N. tabacum* × *N. plumbaginifolia* and *N. tabacum* × *N. glutinosa*. Stamen modifications which prevent proper development of pollen were first noted in the *N. tabacum* × *N. plumbaginifolia* breeding line in a single plant of an otherwise normal BC^2 generation ((T × P) × T) × T. Similarly modified florets were also observed in a single plant of an F_1 generation of an interspecific hybrid, *N. tabacum* × *N. glutinosa*. Repeatedly backcrossing these male-sterile plants to *N. tabacum* resulted in the restoration of *N. tabacum* genomes in *N. tabacum* cytoplasm without altering the expression of male-sterility except in one unusual case. Male-sterile plants from interspecific hybrids involving the cytoplasm of *N. tabacum* and *N. bigelovii* have not been reported heretofore.

Observations

The BC^1 interspecific hybrid generation *4n* (*N. bigelovii* × *N. tabacum*) × *N. tabacum* was extremely uniform with respect to morphology and karyology. In Clayton's[1] hybrids male-sterility was detected in the BC^1, but in this material no evidence of flower distortion or sterility was noted in the BC^1 except for a reduction in the number of viable gametes, which is a characteristic of meiosis in the sesquidiploid generation (BTT). In the BC^2, however, approximately 70 percent of the population showed evidence of a flattened petal-like anther. In this generation some of the plants with distorted anthers also produced variously split corollas. The extent of splitting was the same for all florets for any one plant. However, as day length decreased, the extent of corolla splitting decreased. Conversely, as day length increased, the extent of partitioning of the corolla also increased. Figure 13*A* and *B* illustrates the type of stamens and corollas observed on male-sterile and normal plants of the BC^2 generation.

When a plant with distorted anthers and an entire corolla was used as a maternal parent, the BC^3 progeny developed florets with entire or split corollas and all had the petal-like anther anomaly. If a BC^2 plant which had a split corolla was crossed with *N. tabacum*, then all of the BC^3 progeny developed split corollas. When a BC^2 plant with apparently undistorted anthers (extreme right anther Figure 13*A*) was pollinated with *N. tabacum* then the BC^3 progeny produced florets of the three types illustrated in Figure 13*B*. When this same BC^2 plant was used as a pollen parent and *N. tabacum* acted as the maternal parent, then the progeny of the reciprocal backcross produced normal anthers and corollas. The BC^2 plant, when self-pollinated, produced six male-sterile plants with slight anther distortion and 44 normal plants. Several of these were highly pollen-fertile. A single fertile plant was self-pollinated to produce a BC^2S^2 generation. Fifty plants of the BC^2S^2 were examined; 49 were fully fertile, and one was almost completely sterile, but all 50 plants produced normal florets. Several plants in this generation, including the one with reduced pollen viabil-

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MALE-STERILE AND NORMAL PLANTS
Figure 13

A and *B*—Stamens and corollas of the BC^2 (*N. bigelovii* × *N. tabacum*) × *N. tabacum*. *C* and *D*—Stamens and corollas of the BC^3, (*N. tabacum* × *N. plumbaginifolia*) × *N. tabacum*. *E*—Florets of a male-sterile plant with 48 *N. tabacum* chromosomes on the left, *N. otophora* on the right, and a floret of the F_1 hybrid in the center. *F*—Anthers of a single BC^3 plant (*N. tabacum* × *N. plumbaginifolia*) × *N. tabacum* which produced some fertile pollen.

ity, were examined cytologically. The chromosome arrangement at metaphase of meiosis consisted of 26 bivalents. A highly fertile plant of the BC^2S^2 was then hybridized reciprocally with *N. tabacum*. When this BC^2S^2 was used as a maternal parent, seven normal plants and 43 plants with anther modifications appeared in a 50-plant progeny test. In the reciprocal hybrid, when *N. tabacum* was used as the maternal parent, the 50 plants in the progeny test were normal. Fifty plants of the BC^2S^3 progeny also were normal.

Another male-sterile type was found in a BC^2 generation of (*N. tabacum* × *N. plumbaginifolia*) × *N. tabacum*. In this hybrid, unlike the (*N. bigelovii* × *N. tabacum*) hybrids described above, the cytoplasm of the original F_1 hybrid came from *N. tabacum* which was also used as the recurrent pollen parent in backcrossing. A single plant with petaloid-stigmatoid anthers was observed in a BC^2 progeny ((T × P) × T) × T. The type of distortion was similar to that of the two central stamens, Figure 13*C*. A BC^3 generation (123 plants) was grown to maturity. Most of these (121) developed severe stamen distortions. Of the remaining two plants, one had undistorted anthers and filaments but did not produce fertile pollen. The last plant produced stamens with limited overgrowths of

the filament and anther (Figure 13*F*). This plant was of special interest, because it produced viable pollen and was capable of performing as a paternal parent. It was self-pollinated and hybridized reciprocally. Fifty plants of each progeny were grown to maturity. When the BC^3 plant with normal pollen was used as a maternal parent or when it was self-pollinated, the resulting progenies were male-sterile. However, when it was used as a pollen parent and *N. tabacum* was used as a maternal cytoplasmic-parent, all plants of the progeny were normal. Plants of this reciprocal hybrid generation had meiotic chromosome numbers which varied from 24 bivalents + 2 univalents to 24 bivalents and no univalents. This is in keeping with the chromosome number of the original male-sterile BC^2 plant and the single pollen-fertile BC^3 plant, both of which had 24 bivalents + 2 univalents.

Seven backcross generations beginning with the original male-sterile plant BC^2 ((T × P) × T) × T were obtained. In all these generations, only one plant ever produced sufficient pollen to permit self-pollination and reciprocal hybridization. By the fifth backcross, the diploid chromosome number of the recurrent *N. tabacum* parent was characteristic of all plants of that generation. Only male-sterile plants were produced in the BC^4 through BC^7. Anaphase separations and the appearance of microspore quartets were apparently normal in the BC^5 and subsequent generations. Normal pollen, however, was not produced in the vestigial sporogenous tissue of such modified stamen types as illustrated in Figure 13*C* and *D*, even though meiotic divisions occurred. The petal-like overgrowth of the filament is not as extreme in young stamens as it is in mature florets, and vestiges of sporogenous tissue can be obtained. Often this tissue contains microspore mother cells in various stages of division. The progress of meiotic divisions in the *N. tabacum* × *N. plumbaginifolia* and *N. tabacum* × *N. glutinosa* material was retarded and meiotic stages from prophase through quartets were often found in cells from a single vestigial anther. Modification of the anthers in the *N. bigelovii* × *N. tabacum* material, however, was quite severe and sporogenous tissue was not observed.

The type of stamen modification noted in the F_1 hybrid *N. tabacum* × *N. glutinosa* was similar to that described for *N. tabacum* × *N. plumbaginifolia* in that both the filament and anther were involved. A study of this latter male-sterile (Figure 14*A* and *C*) was relatively uneventful. The F_1 plant (T × G) in which the abnormality occurred was propagated from cuttings. A BC^1 hybrid plant (T × G) × T was obtained by repeatedly pollinating F_1 florets with *N. tabacum* pollen, Figure 14*B* and *D*. This line was carried through seven backcrosses. The male-sterile abnormality occurred in all plants of each generation. A second breeding line was obtained from a colchicine-induced polyploid branch (TT × GG) on an F_1 cutting. This line involved five backcrosses and male-sterile stamen modifications again occurred in every plant of each generation.

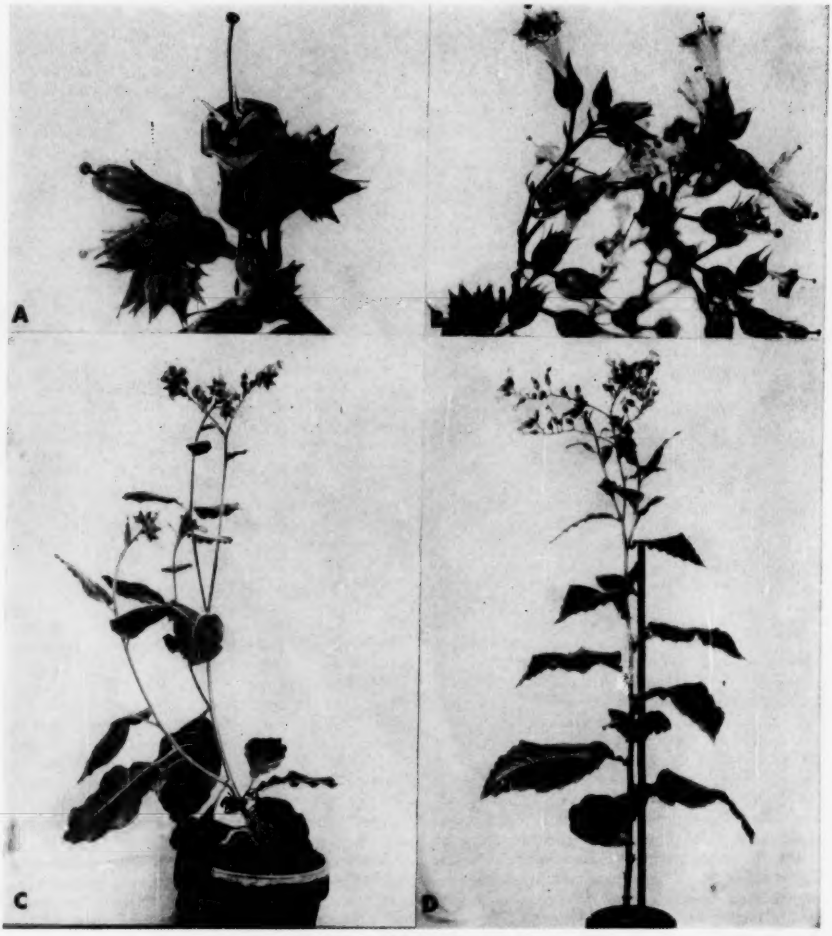
As soon as the chromosome complement of the *N. tabacum* × *N. glutinosa* and *N. tabacum* × *N. plumbaginifolia* lines had been restored to the *N. tabacum* diploid number, several interspecific crosses were made. Male-sterile tobacco plants ($2n = 48$) which originally involved *N. plumbaginifolia* or *N. glutinosa* parentage were crossed with *N. plumbaginifolia, N. glutinosa, N. tomentosiformis,* and *N. otophora*. The behavior of the F_1 hybrid was the same regardless of the source of the male-sterile parent. The crosses of male-sterile *N. tabacum* × *N. plumbaginifolia* produced seeds which germinated, but the seedlings failed to grow. The crosses with *N. glutinosa* produced a few mature plants which were similar to those of other such hybrids involving a normal *N. tabacum* parent except that the hybrids developed with modified stamens. The crosses with *N. tomentosiformis* and *N. otophora* also produced F_1 hybrids which inherited the distorted stamen characteristic of the maternal parent. A floret of the hybrid between a male-sterile maternal and an *N. otophora* paternal parent is illustrated in Figure 13*E*. In this illustration two male-sterile florets appear on the left and a floret of *N. otophora* appears on the right.

Reciprocal grafts were made between male-sterile and normal plants. No changes in anther modifications were noted in the grafted material.

In 1958 a number of residual seed lots of various male-sterile generations were grown in the field and greenhouse. The oldest of these, dating back to 1953, included the original BC^3 generation of the *N. tabacum* × *N. plumbaginifolia* male-sterile. The occurrence of male-sterility and the varying degrees of stamen modification were essentially the same in 1958 as they were in previous years.

Discussion

In the examples of a male-sterile type of anther and corolla distortion from the interspecific combination *N. bigelovii* × *N. tabacum*, flower anomalies appeared in 70 percent of the BC^2 ((B × T) × T) × T generation, concomitant with the appearance of the aneuploid swarm. In this material the allopolyploid (BBTT) and the sesquidiploid, or BC^1, generation (BTT) produced normal progenies. But when the *N. bigelovii* genome (B) was disrupted at anaphase of meiosis in sporophytes of the BC^1, a large number of BC^2 plants developed florets with petal-like anthers; some also developed an apopetalous corolla. The onset of male-sterile flower anomalies could be avoided if *N. tabacum* was



STAMEN MODIFICATION

Figure 14

A—Enlarged view of florets. *B*—Female-fertile but male-sterile florets. *C*—A cutting of the F_1 interspecific hybrid *N. tabacum* × *N. glutinosa*. *D*—The mature BC^1 plant (*N. tabacum* × *N. glutinosa*) × *N. tabacum*.

used as the maternal parent in a cross with a pollen-fertile BC^1 or BC^2 plant. It is interesting that, while all plants with *N. tabacum* cytoplasm were normal, they possessed varying aneuploid chromosome numbers. When a plant of the *N. bigelovii* × *N. tabacum* breeding lines with anther modifications developed, it was completely male-sterile and could, thereafter, be used only as a maternal parent. Some evidence was obtained which suggests that fertile aneuploid ($2n = 52$) forms could be isolated. Such forms might contain 24 *N. tabacum* chromosome pairs and two chromosome pairs from *N. bigelovii* in *N. bigelovii* cytoplasm. However, male-sterile plants would again appear if *N. tabacum* was employed as the pollen parent in a cross with a 52-chromosome plant. Pollen fertility in plants with 48 *N. tabacum* chromosomes was obtained only by introducing tobacco cytoplasm through a reciprocal backcross. Reciprocal hybridization was possible in the *N. bigelovii* × *N. tabacum* and *N. tabacum* × *N. plumbaginifolia* lines. A reciprocal cross was not made in the *N. ta-*

bacum × *N. glutinosa* line because pollen-fertile plants were never obtained in this material.

The type of male-sterile derived from *N. bigelovii* × *N. tabacum* hybrids is not like the types from hybrids which carry *N. tabacum* cytoplasm. Distortions of the flower parts include an apopetalous corolla and petal-like anther modification, but the filament is relatively unaffected, Figure 13*A* and *B*.

It is significant that this type can be reproduced at will. Its occurrence in the BC^2 generation, ((B × T) × T) × T, is entirely predictable. In Clayton's[1] material some male-sterile plants appeared in the BC^1 generation concomitant with the first reduction of *N. debneyi* chromosomes. However, in the *N. bigelovii* × *N. tabacum* hybrids the (B × T) × T sesquidiploid generation was very uniform. The reduction in the number of *N. bigelovii* chromosomes was noted in the BC^2. This reflects the genomic stability of the allopolyploid (BBTT). Therefore, it appears that chromosome inequalities which arise at meiosis in sesquidiploid and later backcross generations may have a role in the induction of male-sterile plants. An immediate exception to this view is the occurrence of stamen modifications in an F_1 hybrid plant (*N. tabacum* × *N. glutinosa*). The chromosome number of this plant was 36, a number normally expected in such a hybrid combination.

Plants with male-sterile flower modifications and the chromosome number and behavior of *N. tabacum* were isolated by repeatedly backcrossing male-sterile plants derived from the hybrids *N. tabacum* × *N. plumbaginifolia* and *N. tabacum* × *N. glutinosa* with *N. tabacum*. These male-sterile tobacco plants were then hybridized with *N. plumbaginifolia, N. glutinosa, N. tomentosiformis,* and *N. otophora*. Mature interspecific hybrids were obtained with all but *N. plumbaginifolia*. Hybrids obtained between the male-sterile tobacco lines and normal *N. species* developed stamen modifications. However, in all other respects, they were equivalent to similar interspecific F_1 hybrids in which the *N. tabacum* parent had normal flowers.

Male-sterile types involving *N. plumbaginifolia* and *N. glutinosa* parentage have been discussed in this report as though they were identical. They are similar in that they originated from single plants in interspecific hybrid progenies in which *N. tabacum* was the cytoplasmic parent. In addition, the extent of stamen modification is similar for both types, including petaloidy of the filaments and stigmatoidy of the anthers. Reports by Goodspeed[2] and Raeber[4] describe or illustrate similar petaloid and petaloid-stigmatoid stamens in exclusively *N. tabacum* germ-plasm. The cytoplasm of a particular *Nicotiana species* may determine the type and extent of flower modifications within rather narrow limits. Observational evidence obtained in this investigation indicates that when flower modifications develop on interspecific hybrids they are characteristic of the cytoplasmic *N. species* parent. The hereditary unit may be a plasmagene which has evolved from, or has been activated by, an interaction of non-specific nuclear components. Such an interaction may occur in F_1 hybrids but is more likely to take place following meiosis in sesquidiploid or later generations.

Summary and Conclusions

Experimental evidence indicating the role of *N. tabacum* and *N. bigelovii* as carriers of a plasmagene for male-sterility is presented. The appearance of the hereditary unit is related to certain interspecific *Nicotiana* hybrids.

Stamen distortions of the various types, discussed in this report, are inherited through the maternal cytoplasm. The extent of flower modification apparently is a function of the *Nicotiana species* involved as the cytoplasmic parent.

The hereditary factor is functional at the cellular level and does not migrate across graft unions like a virus particle. It remained unchanged in seeds stored for five years.

The simple expedient of introducing uncontaminated cytoplasm through reciprocal hybridization between a normal maternal parent and a partially pollen-fertile paternal parent effectively eliminates male-sterile flower modifications. However, when an interspecific plant develops modified flower parts it is male-sterile and thereafter can be used only as a maternal parent.

Repeated backcrossing isolates the factor for anomalous flower parts in plants with the phenotype and chromosome number of the recurrent *N. tabacum* parent. Such plants are completely male-sterile. An attempt to restore fertility in them by wide interspecific hybridizations was not successful.

An attempt to produce a fertile line with only *N. tabacum* chromosomes in the cytoplasm of *N. bigelovii* was unsuccessful.

Literature Cited

1. Clayton, E. E. Male sterile tobacco. *Jour. Hered.* 41:171-175. 1950.
2. Goodspeed, T. H. *Jour. Genet.* 29:327-353. 1934.
3. Koopmans, A. *Genetica* 27:465-471. 1955.
4. Raeber, J. G. and A. Bolton, *Nature* 176:314. 1955.

INHERITANCE OF THE GUINEA TRAIT IN DESCENDANTS OF FLORIDA NATIVE CATTLE

J. C. Dollahon and Marvin Koger*

CATTLE which are known in the southeastern United States as the "guinea" were described in an earlier study by Koger *et al.*[5] as compact, short-legged individuals which attain approximately two-thirds the size of normal cattle. Certain guinea animals give the impression of possessing unusual vitality and the ability to thrive under adverse nutritional conditions. This appearance has led to considerable interest in the animals among cattle producers.

In many respects the guinea observed in crossbred and Florida native cattle resembles phenotypically the Dexter described by Crew[1], the "Comprest" in Herefords described by Woodward *et al.*[7], the "Compact" observed in Shorthorns by Stonaker and Tom[6], and the "Midget" which occurs in the American Brahman[4]. Since such a similarity existed, it was decided to include the guinea in a study on various forms of dwarfism in cattle.

The "bulldog" lethal which occurs commonly in Dexter cattle was described by Crew[1]. Although a private breeder reported to the authors having observed Dexter-type bulldog dwarfs produced from guinea × guinea matings in Florida, such observations have not been reported in scientific literature.

Procedure

Beginning in 1951 one of the authors (M.K.) began recording observations in certain commercial herds on the phenotype of offspring from guinea animals†. When guinea calves were observed, an attempt was made wherever possible to record the phenotype of the dam and of the sire when the male parent was known.

During 1955 and 1956 eight females and two guinea bulls of distinct guinea type were purchased from private breeders to be placed in experimental breeding herds where the animals could be kept under close observation. During 1956 and 1957 five guinea females became pregnant when mated to guinea bulls. The females were checked for pregnancy after exposure to bulls for 90 days. The phenotype of the calves was recorded at birth and periodically thereafter until classification of phenotype was definitely established.

Results and Discussion

A summary of the information obtained by recording phenotype of animals in private herds is shown in Table I. The phenotypic ratios resulting from the two types of matings shown strongly suggest that the guinea phenotype is the result of a semi-dominant lethal gene.

TABLE I. Phenotypic classification of the progeny of guinea × guinea and guinea × normal matings which were made in private herds

Mating	Total number of progeny	Percent guinea progeny	Percent normal progeny
Guinea × Normal	84	48	52
Guinea × Guinea	32	72	28

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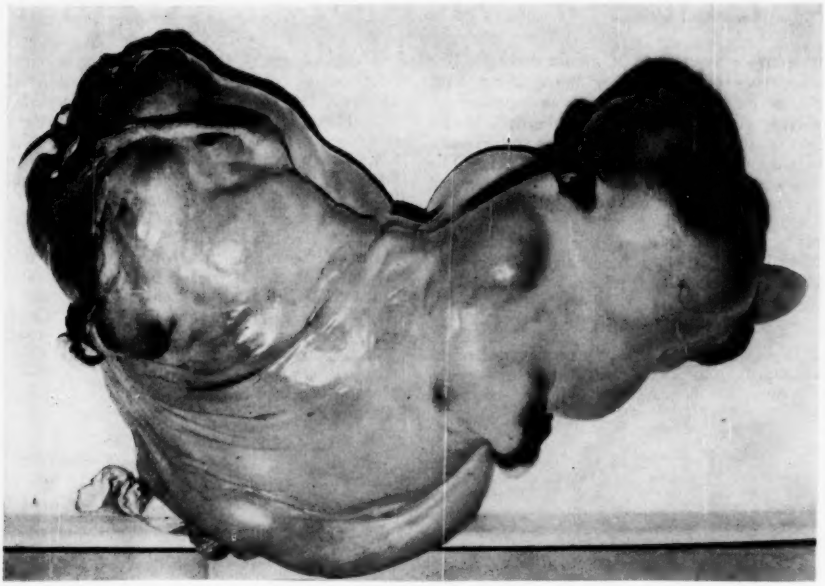
†Sincere appreciation is expressed especially to Mr. Ralph Sexton of Vero Beach, Florida, and Mr. J. A. Pancoast, Uleta, Florida, for making their herds available for these observations and for making available animals for test matings.



DEXTER-TYPE BULLDOG CALF

Figure 15

A bulldog calf produced from a guinea × guinea mating. Note the shortened limbs and the general abnormal proportions of the fetus.

It is suggested that the absence of recorded lethals from guinea × guinea matings is due to early abortion or resorption of the fetuses. This hypothesis is substantiated by the results of guinea matings in the experimental herd. From a total of five guinea × guinea matings, three types of offspring were produced: 1) a normal non-guinea, 2) one typical guinea calf, and 3) a Dexter-type bulldog dwarf as shown in Figure 15. This fetus was aborted after a gestation of approximately seven months. The dam was in labor for only a short time and recovered quickly without visible evidence of lactation. Had the attendant failed to be present, it is probable that the bulldog would have gone unrecorded. This observation may explain why ranchers generally report no bulldog calves from guinea × guinea matings. Two guinea cows which had been mated to a guinea bull were diagnosed as pregnant at approximately the third and fifth months of gestation, respectively. Neither of the females calved at the expected time and upon examination during the tenth month following breeding were opened. Apparently these two animals either aborted or resorbed the fetuses.

From the phenotypic ratios which were observed in private herds and the apearance of the typical Dexter-type bulldog lethal in offspring from the experimental matings, it is concluded that the guinea condition is due to the presence of a semi-dominant lethal gene in the heterozygous condition. There was a striking resemblance between the bulldog produced in this study and those produced from Dexter matings[3]. Since importation of Dexter cattle into Florida occurred prior to 1900, the Florida guinea probably is a descendant of Dexter cattle as suggested by Dollahon[2].

A number of guinea-like animals have been produced by mating comprest and dwarf bulls to females of mixed breeding. Guineas are presently being crossed with comprest type Hereford and Angus animals, midget Brahman and snorter dwarfs to investigate the genetic relationship of the guinea to these forms of dwarfism.

Summary and Conclusions

The inheritance of a trait known as guinea among descendants of Florida native cattle has been investigated. The typical guinea is a compact, short-legged individual which attains approximately two-thirds the size of normal individuals of similar breeding. A typical Dexter-type bulldog lethal occurred among the

progeny of five guinea × guinea matings. The occurrence of this bulldog lethal along with phenotypic ratios resulting from matings involving guinea cattle in private herds indicates that the guinea phenotype is due to the presence of a semi-dominant "bulldog" lethal gene. The striking resemblance of the bulldog produced in this study to that reported in the progeny of Dexter animals, along with the fact that Dexter cattle were introduced into Florida prior to 1900, suggests that the guinea is a descendant of the Dexter.

Literature Cited

1. Crew, F. A. E. The significance of an achondroplasia-like condition met with in cattle. *Proc. of the Roy. Soc. of London.* Series B. 1923.

2. Dollahon, J. C. Genetic and anatomical relationships of dwarf cattle. Unpublished Master's Thesis. University of Florida. 1956.

3. Hutt, F. B. Inherited lethal characters in domestic animals. *Cornell Vet.* 24:1. 1934.

4. Koger, M. Midgetism in the American Brahman. *International Brahman Review* 3:6. 1957.

5. Koger, M., J. C. Dollahon, A. C. Warnick, W. G. Kirk, J. F. Hentges and A. Z. Palmer. Forms of dwarfism in English and Brahman breeds of beef cattle. *Jour. Animal Sci.* 14:1186. 1955.

6. Stonaker, H. H. and R. C. Tom. "Compact" shorthorns. *Jour. Hered.* 35:247. 1944.

7. Woodward, R. R., R. T. Clark and J. N. Cummings. Studies on large and small type Hereford cattle. *Montana Agric. Exp. Sta. Bul.* 401. 1942.

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An Efficient Technique for Making Crosses Between Annuals and Perennials

PLANT breeders are often faced with the time-consuming aspects of hand manipulation of floral parts in making crosses. Where emasculation is difficult, the number of flowers pollinated is often not sufficient to ensure a successful cross. In addition, numerous other complications such as mechanical damage to the carpels and petioles, deleterious effects of bagging, and protection of bagged portions of the plant against the elements under field conditions, all operate against the possibility of a successful cross. The polycross technique minimizes most of these problems; however, a more serious problem often arises in using this technique—that of distinguishing the true hybrids in segregating populations.

A useful method for recognizing true hybrids from selfs among polycross progeny has been noted recently in a cross between an annual and a perennial species of the genus *Alopecurus.* The characteristics of these grasses were sufficiently distinct to assume that hybrid plants could be recognized in a polycross progeny. The first year's growth of the polycross seed taken from the annual parent revealed no obvious hybrids. However, hybrid seed was apparently present as the second growing season revealed that the first winter had removed all of the parental annual plants, leaving only a few perennial plants. These few plants closely resembled the annual parent, with the exception of being perennial. In this particular cross hybridity was further confirmed since the parents differed in chromosome number and the hybrids carried the expected intermediate number.

In theory this technique should operate as well in all crosses where one parent is an annual and the other a perennial and where perennialism persists in the F_1.

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INHERITANCE OF FEMALE STERILITY IN SORGHUM

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THE female sterility in sorghum referred to herein was first observed at Manhattan in 1947. It was noted that unexpected sterility, 100 percent in some cases, was occurring in certain F_1 populations resulting from crosses between male sterile (ms_2) × Early Kalo lines and the recurrent parent, Early Kalo[3]. This sterility differed from ms_2 in that anthers that shed pollen were produced. The stigma, style and ovary were only rudimentary and female sterility was complete with no seed being set even in the presence of pollen (Figure 16). Such female-sterile plants functioned normally as male parents in controlled crosses (Figure 17).

Female-sterile plants can be identified at time of anthesis. The glumes of the female-sterile plants only partly open, and the anthers are not exserted but remain between the glumes and usually do not shed their pollen. However, the pollen pours out if the florets are inverted. After the normal period of anthesis in the morning, the glumes close and pinch the anthers between them.

Inheritance studies were started in 1949, using the original ms_2 material. These studies suggested that this female sterility in sorghum is caused by a complementary effect of dominant genes. It also was learned that another type of sterility, probably differing more in degree than kind, is involved in the genetic system that controls female sterility. This latter type of sterility is manifested in abnormal dwarf plants which produce no heads. These studies also showed that all lines of Early Kalo do not possess genes for female sterility.

In 1950, crosses were made between Early Kalo,231, the line involved in the

NORMAL AND FEMALE-STERILE HEADS OF SORGHUM

Figure 16

Normal head with full seed set (left), and pollinated female-sterile head with no seed set (right).

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original female-sterile F_1 population, and several other sorghum varieties. None of the material in these crosses carried the ms_2 factor. This paper reports on the inheritance of female sterility in these crosses[1, 2]. The suggested genes involved are $Fs_1Fs_1fs_2fs_2$ in Early Kalo,231, and $fs_1fs_1Fs_2Fs_2$ as the complementary genes in the other varieties.

Materials and Methods

Early Kalo,231 was used as the pollen parent in crosses with an unnamed selection from the cross Dwarf White Milo × Blachull Kafir and with the varieties Double Dwarf Yellow Sooner (S.A. 5155-36), Farr's Feterita, Pink Kafir, Western Blackhull, Norghum, Westland and Ellis. The F_1 progenies of these crosses were grown in the field in 1951.

Female-sterile F_1 plants were used as pollinators in backcrosses with both parents of the Westland, Pink Kafir and Western Blackhull crosses. This resulted in six backcrosses which were grown in the field in 1952 (Table I).

Testcrosses were made in the field in 1952 and in the greenhouse in 1953. In these testcrosses, one of the 1952 BC_1 progenies, Early Kalo × *fs*(Westland × Early Kalo,231, F_1), was used as the male parent, and Westland and Early Kalo,231 were used as female parents. The progenies of these testcrosses were grown in the field in 1956.

Results and Discussion

Of the F_1 progenies grown in the field in 1951, crosses between Early Kalo,231 and Westland, Pink Kafir and Western Blackhull produced female sterility. However, not all plants of the varieties used as female parents produced female-sterile progeny. The results of these crosses are as follows:

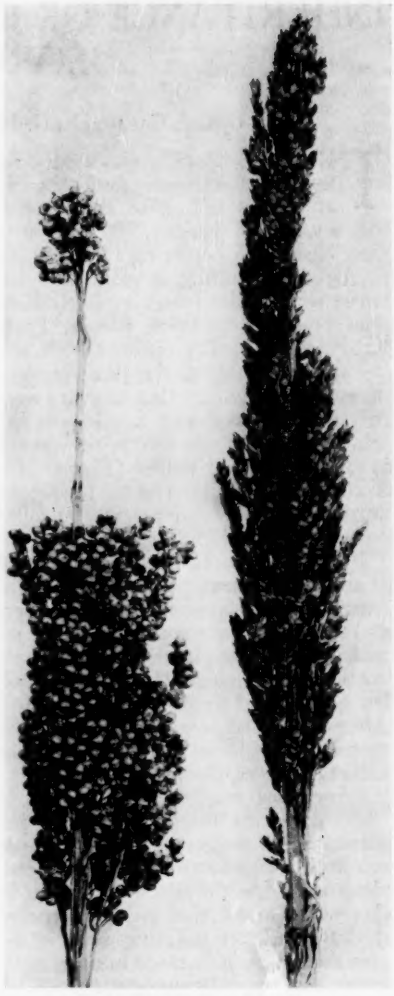
Westland × Early Kalo,231
- Cross No. 1—All F_1 plants fertile.
- Cross No. 2—All F_1 plants female-sterile.

Pink Kafir × Early Kalo,231
- Cross No. 1—All F_1 plants fertile.
- Cross No. 2—All F_1 plants female-sterile.

Western Blackhull × Early Kalo,231
- Cross No. 1—Some F_1 plants fertile, some female-sterile.
- Cross No. 2—All F_1 plants female-sterile.

It was concluded that the three varieties, Westland, Pink Kafir and Western Blackhull, are heterogeneous for the Fs_2 factor, and that by chance both a homozygous dominant and a homozygous recessive plant were used in the case of Westland and Pink Kafir, and a homozygous dominant and a heterozygous plant in the case of Western Blackhull.

None of the F_1 progenies involving Dwarf White Milo × Blackhull, Double Dwarf Yellow Sooner, Norghum, or Ellis displayed fe-



CONTROLLED CROSS

Figure 17

Seed at the tip of normal head (left) was produced by pollinating hand-emasculated florets with pollen from female-sterile head (right).

male sterility. This might lead to the conclusion that these varieties do not carry the gene Fs_2. However, it should be pointed out that only one plant of Norghum and Ellis and two plants of the other two varieties were used in the crosses. This leaves the possibility that these varieties are heterogeneous for the Fs_2 factor, as in Westland, Pink Kafir and Western Blackhull, and by chance only homozygous recessive plants were used in the crosses.

The F_1 progenies of the crosses involving Farr's Feterita headed very late in the season and appeared to be sterile. However, since it is known that weather conditions prevailing in late September and October at Manhattan can cause sterility in sorghums, it could not be determined with certainty whether the sterility was true female sterility or was induced by weather conditions.

Data relative to the BC_1 progenies, resulting from the crosses made in 1951 and grown in 1952, are given in Table I. The data from the Early Kalo,231-Westland backcrosses and the Early Kalo,231-Pink Kafir backcrosses support the hypothesis that female sterility is the result of a complementary effect of dominant genes ($Fs_1fs_1Fs_2fs_2$). This is manifested as complete sterility in dwarf, headless plants when three genes are in the dominant condition ($Fs_1Fs_1Fs_2fs_2$ or $Fs_1fs_1Fs_2Fs_2$). It is assumed that the homozygous, double dominant, $Fs_1Fs_1Fs_2Fs_2$, would produce dwarf, headless plants, but such a genotype cannot be recovered. One of the Early Kalo,231-Western Blackhull backcrosses supports the above hypothesis, but the other one does not, evidenced by the chi-square value, 8.07, P = .01-.025. However, both Early Kalo,231-Western Blackhull backcrosses deviate from the expected in the same manner in that there is a deficiency of normal plants. This might lead one to suspect the presence of other genetic complications for female sterility in Western Blackhull. Further study is necessary to establish definitely the genotype of Western Blackhull with respect to female sterility. In all crosses there is a tendency for a deficiency of dwarf plants in relation to expected numbers. Inasmuch as the sterility being dealt with probably is an abnormality involving physiological deficiencies, it may not be illogical to postulate that seeds having the genotypes ($Fs_1Fs_1Fs_2fs_2$ or $Fs_1fs_1Fs_2Fs_2$) for dwarfness and headlessness are low in germination or seedling survival.

Data from the testcrosses grown in the field in 1956 are given in Table II. The data further substantiate the hypothesis regarding female sterility. In the testcrosses with Westland as the female parent, only normal BC_1 plants were used. However, these normal plants could have been of the genotype $Fs_1Fs_1fs_2fs_2$ or the genotype $Fs_1fs_1fs_2fs_2$, and should occur in the ratio of 1:1. If the genotype were $Fs_1Fs_1fs_2fs_2$, only female-sterile plants should be obtained in the testcross progeny, and if $Fs_1fs_1fs_2fs_2$ were the genotype, both normal and female-sterile plants should occur in a ratio of 1:1. Only female-sterile plants occurred in Crosses No. 1 and 2, and it can be concluded that the male parents involved were of the genotype $Fs_1Fs_1fs_2fs_2$. Both normal and female-sterile plants occurred in Crosses No. 3, 4, 5, 6 and 7 in a ratio approaching the expected 1:1 ratio. Projecting these results back to the BC_1 prog-

TABLE I. Segregation for normal, female-sterile, and dwarf plants in the first backcross progenies of crosses involving the sorghum varieties Early Kalo, Westland, Pink Kafir and Western Blackhull

Parentage of BC_1 progenies	Total plants	Phenotype of plants: Normal	Female-sterile	Dwarf	Chi-* square	P-values
	no.	no.	no.	no.		
Early Kalo,231-Westland Backcrosses						
Early Kalo,231 × fs(Westland × Early Kalo,231, F_1)	91	42	28	21	1.62	.25-.50
Westland × fs(Westland × Early Kalo,231, F_1)	78	42	21	15	1.38	.50
Sum of 2 chi-squares					3.00	.50-.75
Pooled chi-square	169	84	49	36	2.01	.25-.50
Early Kalo,231-Pink Kafir Backcrosses						
Early Kalo,231 × fs(Pink Kafir × Early Kalo,231, F_1)	38	20	11	7	0.95	.50-.75
Pink Kafir × fs(Pink Kafir × Early Kalo,231, F_1)	28	18	5	5	2.29	.25-.50
Sum of 2 chi-squares					3.24	.50-.75
Pooled chi-square	66	38	16	12	2.00	.25-.50
Early Kalo,231-Western Blackhull Backcrosses						
Early Kalo,231 × fs(Western Blackhull × Early Kalo, 231, F_1)	45	19	17	9	3.93	.10-.25
Western Blackhull × fs(Western Blackhull × Early Kalo,231, F_1)	30	9	14	7	8.07	.01-.025
Sum of 2 chi-squares					12.00	.01-.025
Pooled chi-square	75	28	31	16	10.81	.005

*Chi-square calculations based on an assumed 2(normal):1(female-sterile):1(dwarf) ratio.

eny, it is found that a random sampling of the normal plants yielded two $Fs_1Fs_1fs_2fs_2$ genotypes and five $Fs_1fs_1fs_2fs_2$ genotypes which can be assumed to fit the expected 1:1 ratio (chi-square, 1.28, P = .25-.50).

The data from the testcrosses involving Early Kalo,231 and normal BC_1 plants (Crosses No. 8, 9, 10, 11, 12, 13 and 14) offer little aid in identifying the genotype of the normal BC_1 plants. However, since only normal plants occurred as expected in the progenies, it can be said that the normal BC_1 plants were not of a genotype other than $Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$.

Summary

Data from F_1, BC_1, and testcross progenies resulting from Early Kalo,231-Westland crosses and Early Kalo,231-Pink Kafir crosses show that the complementary effect of two dominant genes (Fs_1 and Fs_2) result in female sterility when in the double heterozygous condition ($Fs_1fs_1Fs_2fs_2$). When three dominant genes are present ($Fs_1Fs_1Fs_2fs_2$ or $Fs_1fs_1Fs_2Fs_2$), dwarf plants occur that do not produce heads. It is assumed that the double homozygous dominant condition ($Fs_1Fs_1Fs_2Fs_2$) also would result in dwarf, headless plants, if it were possible to recover this genotype.

The sorghum variety Early Kalo carries one of the complementary genes (Fs_1) and the Westland, Pink Kafir and Western Blackhull varieties carry the other (Fs_2). However, these four varieties carry the respective genes in the heterogeneous condition. Neither the Fs_1 nor the Fs_2 gene has any apparent effect when occurring alone.

Literature Cited

1. Casady, A. J. Annual Report Sorghum Breeding and Testing Project. Kansas State College, Manhattan, Kansas. 1956.

2. Heyne, E. G. and D. E. Weibel. Annual Reports of Small Grain and Sorghum Breeding Project. Kansas State College, Manhattan, Kansas, 1948, 1949, 1950, 1951 and 1952.

3. Stephens, J. C. Male sterility in sorghum: Its possible utilization in production of hybrid seed. *Jour. Amer. Soc. Agron.* 29:690-696. 1937.

TABLE II. Segregation for normal, female-sterile and dwarf plants in testcross progenies of crosses involving the sorghum varieties Early Kalo and Westland

Cross no.	Phenotype of male parent	Genotype of female parent	Possible genotypes of male parent	Total plants	Phenotype of plants: Normal	Female-sterile	Dwarf	Chi-square	P-values
				no.	no.	no.	no.		
	Westland × [Early Kalo, 231 × *fs*(Westland × Early Kalo, 231, F_1), MC_1]								
1	Normal	$fs_1fs_1Fs_2Fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	24	0	24	0		
2	Normal	$fs_1fs_1Fs_2Fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	27	0	27	0		
3	Normal	$fs_1fs_1Fs_2Fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	2	1	1	0	0	
4	Normal	$fs_1fs_1Fs_2Fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	10	5	5	0	0	
5	Normal	$fs_1fs_1Fs_2Fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	18	11	7	0	0.88	.25-.50
6	Normal	$fs_1fs_1Fs_2Fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	6	6	0	0	6.00	.01-.025
7	Normal	$fs_1fs_1Fs_2Fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	9	2	7	0	2.78	.05-.10
			Sum of 5 chi-squares					9.66	.25-.50
			Pooled chi-square	45	25	20		0.56	.25-.50
	Early Kalo, 231 × [Early Kalo, 231 × *fs*(Westland × Early Kalo, 231, F_1), BC_1]								
8	Normal	$Fs_1Fs_1fs_2fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	58	58	0	0		
9	Normal	$Fs_1Fs_1fs_2fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	38	38	0	0		
10	Normal	$Fs_1Fs_1fs_2fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	8	8	0	0		
11	Normal	$Fs_1Fs_1fs_2fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	43	43	0	0		
12	Normal	$Fs_1Fs_1fs_2fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	30	30	0	0		
13	Normal	$Fs_1Fs_1fs_2fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	14	14	0	0		
14	Normal	$Fs_1Fs_1fs_2fs_2$	$Fs_1Fs_1fs_2fs_2$ or $Fs_1fs_1fs_2fs_2$	17	17	0	0		

"SILKY," A DOMINANT MUTATION IN SHEEP

B. L. Warwick, S. P. Davis, R. O. Berry and R. E. Patterson*

SILKY AND NON-SILKY SHEEP

Figure 18

A—The original "freak buck" which was alleged to be a sheep × goat hybrid. It was a dominant mutation which has been named "silky." This ram was heterozygous (*Ss*). *B*—Silky ewes (*Ss*) sired by the ram in *A* and out of non-silky dams (Merinos). *C*—Silky ram (*Ss*) from silky dam (*Ss*) × non-silky sire (*ss*). *D*—Non-silky segregate (*ss*).

IN the early thirties, there was born on a large West Texas ranch, a "freak buck" from a range-bred Delaine-Merino ewe. This was alleged to be a natural hybrid, with an Angora goat as the sire. Study of the original "freak buck" and some of his female offspring showing the same characteristics, together with later generations, has led to the hypothesis that this was a dominant mutation and not a sheep × goat hybrid. A popular article[9] which included pictures of some of the these animals was published. The purpose of this paper is to give a more detailed description and history of this mutation and the breeding

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evidence on which conclusions are based.

The "freak buck" was assumed to be the offspring of an Angora male goat because both sheep and Angora goats were pastured together, as is common practice in Texas, and his fleece had some of the characteristics of mohair. This, together with the shaggy appearance of the animal, led the rancher to believe that it *must* have been the result of natural mating of the mother ewe with one of the Angora bucks. In 1932 the man then in charge of that ranch turned the "freak buck" into a pasture with several hundred ewes. No other male was in the pasture until the "freak buck" was taken out and castrated. The son of the late owner of the ranch said that about 70 lambs were dropped from these matings and that a large number (he thought about 50) closely resembled their sire. All the males were castrated before weaning, and all the "freak" lambs were sold to a livestock dealer from whom we purchased 12 ewes for further study and breeding. By this time these animals had been widely publicized in the newspapers under the name of "Geet."

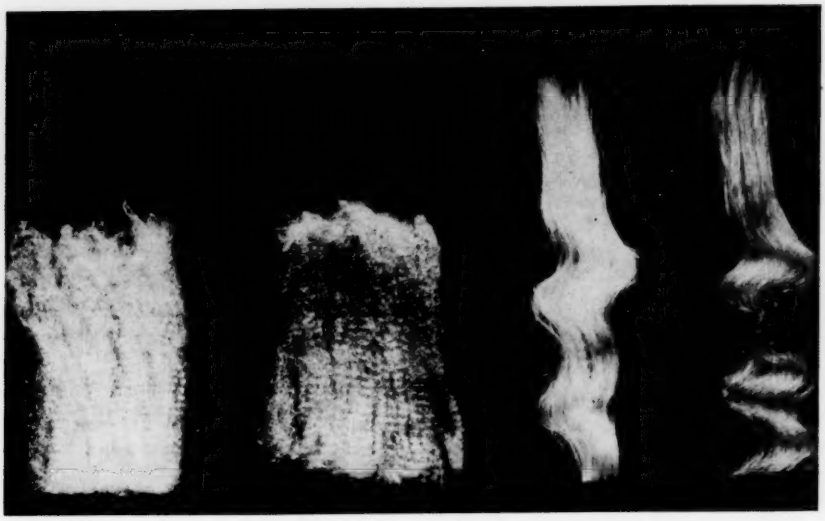
The most marked characteristics of the fleeces were: (a) absence of distinct crimp, the locks resembling flat locks of mohair with large bold waves instead of the crimp so characteristic of Merino wool, (b) marked tendency to partly shed, resulting in extreme "cotting" or felting of many of the fibers before shearing[6], (c) extreme greasiness, (d) diameter of fiber in microns was within the range of 64's to 80's wool, (e) scales on the fibers were similar to those on Merino wool fibers, and (f) absence of halo hairs[2, 7] in the birth coat. The shorn fleece was difficult to pull apart. The cotting was less noticeable in six-months fleeces. Halo hairs in Merino and Rambouillet sheep are medullated or partly medullated fibers produced by the primary hair follicles, partly extend beyond the surface of the main birth coat and are normally shed within a few weeks of birth. Fibers of the birth coat of the mutant type were non-medullated, smooth covering at birth of normal lambs of and wavy rather than spiral. The wooly wool producing breeds, British breeds as well as Merino, consists of spiral or curly tufts of fibers[1]. Histological study of skin sections for comparison with the normal[5] revealed marked thickening of the epithelium and extreme irregularity in the arrangement of all follicles. Also, all or most of the primary follicles were degenerate. The slick, shining appearance of the newborn lamb led us to use the term "silky" for this mutation.

Other than in fleece characteristics, these animals differed from parental fine wool sheep only in that they had no skin folds[3]. They were similar to sheep in tail length, tail carriage and infra-orbital glands[4]. Also, the males had horns and the females had knobs typical of Merino and Rambouillet sheep[10]. At the same time that we secured the "silky" ewes, attempts were made at this station to produce hybrids from sheep and goats[8]. We had a fertile male goat which we had raised on a sheep foster mother so that we could secure natural matings to sheep. The male goat was bred many times over a period of two breeding seasons to one of the "silky" ewes, but the "silky" ewe always came in estrus again in about 17 days. Late in the breeding season she

TABLE I. Breeding results

Dams	Sires	Progeny		Totals
		Silky (*S*-)	Non-silky (*ss*)	
Silky (*Ss*)	Silky (*Ss*)	13	5	18
Silky (*Ss*)	Non-silky (*ss*)	2	3	5
Non-silky (*ss*)	Silky (*Ss*)	16	15	31
	Totals	18	18	36
Non-silky (*ss*)*	Non-silky (*ss*)*	0	9	9

*Non-silky segregates.



SILKY AND NON-SILKY LOCKS

Figure 19

Two locks from silky (right) and two locks from non-silky segregate (left). Dams of both animals were silky. The left lock of each pair has been cleaned with CCl_4.

was bred to a "non-silky" ram and produced a normal "non-silky" lamb. In succeeding seasons she was bred to "silky" rams and gave birth to "silky" lambs. Our attempts to cross sheep and goats resulted in fertility but no live births[11]. Also, the manager of the ranch from which the "freak buck" came tried later to mate the Angora buck (which was alleged to be the sire of the original "freak buck") to ewes without success. These observations made it extremely doubtful that the "freak buck" was a natural hybrid as alleged.

The vitality of these "silky" sheep was poor. Of the 12 "silky" ewes purchased for experiment, only six gave birth to lambs before they died. There were 31 "silky" lambs born from parents, one or both of which were "silky," yet it was impossible to maintain a stock of "silky" breeding ewes, and so the breeding experiment ended with the disposal of the last "silky" ram.

The observations on the ranch where the original "freak buck" was born were suggestive of this character being due to a dominant mutation. Using this hypothesis, the "silky" ewes which we purchased would be heterozygous (*Ss*). Offspring from these (*Ss*) × Rambouillet rams (*ss*) produced both "silky" (*Ss*) and "non-silky" (*ss*) offspring. One of these silky" (*Ss*) males was used for breeding to the above ewes (*Ss*). Both "silky" (*S*-) and "non-silky" (*ss*) offspring were born. Two of the "silky" (*S*-) male offspring were used for breeding, to both "silky" and "non-silky" ewes. Each produced both "silky" and "non-silky" lambs, proving that these sires were heterozygous (*Ss*). The "silky" ewes which were sired by "non-silky" rams were heterozygous (*Ss*). "Silky" ewes which were the offspring of "silky" sire × "silky" dam each produced both "silky" and "non-silky" lambs, proving that they were heterozygous (*Ss*). Matings of heterozygotes (*Ss*) × heterozy-

SILKY AND MERINO WOOL FIBER

Figure 20

Silky fiber from side, (left), and 70's Merino wool fiber, (right), to show similarity of scales.

gotes (*Ss*) produced 13 "silky": 5 "non-silky." Heterozygotes (*Ss*) × "non-silky" (*ss*) gave a perfect 1:1 ratio of "silky": "non-silky." "Non-silky" segregates bred *inter se* produced only "non-silky" progeny, (Table I).

Summary and Conclusions

A dominant mutation in Merino sheep is described and the breeding data on which this hypothesis is based are given. The mutation is called "silky" because of the appearance of the newborn lambs, which were devoid of halo hairs, had smooth wavy wool and had no skin folds. The fleeces of the adults showed only broad waves in the locks rather than the crimp so characteristic of wool from Merino and Rambouillet sheep. The viability of the mutants was very poor.

Literature Cited

1. DUERDEN, J. E. Waves in wool. How the crimps are produced. *The Farmer's Weekly* (South Africa). 4 pp. Nov. 17, 1926.

2. ————. Evolution in the fleece of sheep. *S. African Jour. Sci.* 24:388-415. 1927.

3. JONES, J. M., B. L. WARWICK, R. W. PHILLIPS, D. A. SPENCER, C. B. GODBEY, R. E. PATTERSON and W. H. DAMERON. Inheritance of skin folds on sheep. *Jour. Animal Sci.* 5: 154-169. 1946.

4. LYDEKKER, R. The Sheep and Its Cousins. Allen, London. 1912.

5. PATTERSON, R. E. A study of hair follicles and their changes as related to wool characteristics. Ph.D. Thesis. A. & M. College of Texas. 1943.

6. ROBERTS, J. A. FRASER. The cotted fleece. *Jour. Textile Inst.* 17:T171-T179. 1926.

7. SCHINCKEL, P. G. Birthcoats of Australian Merino lambs. *Nature* 168:698-699. 1951.

8. WARWICK, B. L., R. O. BERRY and W. R. HORLACHER. Results of mating rams to Angora female goats. *Proc. Amer. Soc. Animal Production* pp. 225-227. 1934.

9. ———— and W. H. DAMERON. Crossing sheep and goats. *Southwestern Sheep and Goat Raiser* 7:8 and 22. 1937.

10. ———— and P. B. DUNKLE. Inheritance of horns in sheep. *Jour. Hered.* 30:325-329. 1939.

11. ———— and R. O. BERRY. Intergeneric and intra-specific embryo transfers in sheep and goats. *Jour. Hered.* 40:297-303. 1949.

THE NATURE OF POLYPLOIDY IN SMOOTH BROMEGRASS

***Bromus inermis* Leyss.**

H. L. CARNAHAN AND HELEN D. HILL*

CYTOLOGICAL studies designed to reveal the nature of polyploidy in the cytologically difficult octoploid *Bromus inermis* have not been conclusive[1, 2, 3]. Information on the inheritance of qualitative characters would also provide evidence on the nature of polyploidy in the species, but no such reports are available in the literature.

From an earlier investigation the authors[3] reported the meiotic behavior of hexaploid *Bromus inermis* plants derived from a cross between a polyhaploid ($2n = 28$) and an octoploid ($2n = 56$). The fertile polyhaploid (tetraploid) parent was obtained from a plant introduction of uncertain origin. The tetraploid therefore could have been either a polyhaploid or a plant from a tetraploid race of the species. Consequently, the essentially triploid meiotic behavior observed in hexaploids and the "normal" meiosis of an unexpected octoploid[3] could have resulted from either of the two following genome relationships at the three levels of polyploidy:

(*a*) polyhaploid ($2n = 28$) parent	$A_1A_1\ B_1B_1$
normal octoploid parent	AAAA BBBB
hexaploid F_1	$AAA_1\ BBB_1$
octoploid F_1 (unreduced + reduced gamete)	$AAA_1A_1\ BBB_1B_1$
or	
(*b*) polyhaploid parent	AA BB
normal octoploid parent	AAAA BBBB
hexaploid F_1	AAA BBB
octoploid F_1 (unreduced + reduced gamete)	AAAA BBBB,

where A and B represent two distinct genomes, and chromosomes of genomes A_1 and B_1 are similar to A and B genomes, respectively, but sufficiently differentiated structurally to impair pairing.

Frequencies of micronuclei as a consequence of unpaired chromosomes in F_1 derived octoploid × normal octoploid plants should provide a basis for preferring one of the genome models to the other. If model *a* were correct, the F_1 octoploids would be $AAAA_1\ BBBB_1$ and they should be characterized by less meiotic regularity, i.e., more micronuclei than normal *B. inermis*. On the other hand, normal meiotic behavior of octoploid F_1 plants would provide evidence supporting model *b*, and these plants would have the genome formula AAAA BBBB.

Materials and Methods

An exceptional octoploid plant, designated clone 23, occurred in a predominantly hexaploid F_1 population from the cross polyhaploid ($2n = 28$) × normal octoploid *B. inermis*. Clone 23 is presumed to have arisen by fertilization of an unreduced egg of the polyhaploid by a sperm with reduced chromosome complement from the octoploid parent. Clone 23, hereafter designated the "derived octoploid," was used as the maternal parent and pollinated with a composite of pollen from several representative normal octoploid plants.

Twenty-six F_1 plants, derived octoploid × normal octoploid, were grown in the greenhouse. Panicles were fixed in 6:3:1 Carnoy's solution of alcohol, chloroform and acetic acid. Micronuclei were counted in 100 or more quartets from each F_1 plant.

Chromosome numbers of clones 23-7 and 23-10 were determined from root-

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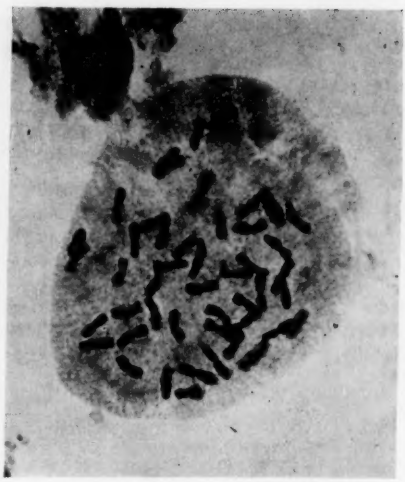
tips pre-treated in Para-Dichloro-Benzene for two hours at 15° C and then fixed and smeared in aceto-orcein.

Results and Conclusions

Percentages of quartets free of micronuclei and mean numbers of micronuclei per quartet for the 26 F_1 derived octoploid × normal octoploid plants are given in Table I. Considerable variation among plants existed for these cytological characteristics, but the variation was well within the limits observed for the species[1, 2, 4]. Two F_1 plants, 23-7 and 23-10, had micronuclei frequencies comparable with those reported by Schertz and Murphy[4] for plants with aneuploid chromosome complements. Chromosome numbers of 23-7 and 23-10 were 56 and 50, respectively (see Figure 21). Eleven other random F_1 plants were found to be $2n = 56$.

The normal frequencies of micronuclei in quartets of the F_1 octoploids support the contention that chromosomes from the polyhaploid parent are similar enough to those in octoploid *B. inermis* that they did not contribute to higher than expected micronuclei frequencies in F_1 hybrids. These results, together with those of Hill and Carnahan[3] and work cited by them, are in harmony with the interpretation that octoploid *B. inermis* is an autoallopolyploid, AAAA BBBB, in which considerable, but far from complete, diploidization has occurred.



CHROMOSOME COMPLEMENT

Figure 21

Root-tip cell of clone 23-10 showing somatic complement of 50 chromosomes. Magnification ca. 1000×.

Literature Cited

1. Elliott, F. C. The cytology and fertility relations of *Bromus inermis* and some of its relatives. *Agron. Jour.* 41:298-303. 1949.

2. ———— and R. M. Love. The significance of meiotic chromosome behavior in breeding smooth bromegrass, *Bromus inermis* Leyss. *Jour. Amer. Soc. Agron.* 40:335-341. 1948.

3. Hill, Helen D. and H. L. Carnahan. Karyology of natural 4×, 6× and 8× progenies of a tetraploid (4×) clone of *Bromus inermis* Leyss. *Agron. Jour.* 49:449-452. 1957.

4. Schertz, K. F. and R. P. Murphy. Fertility in relation to chromosome constitution and behavior in *Bromus inermis* Leyss. *Agron. Jour.* 50:372-376. 1958.

TABLE I. Percentage of quartets free of micronuclei and mean number of micronuclei per quartet in 26 F_1 plants of the cross, derived octoploid × normal octoploid *B. inermis*

F_1 Plant	Quartets free of micronuclei	Mean micronuclei per quartet	F_1 Plant	Quartets free of micronuclei	Mean micronuclei per quartet
	%	No.		%	No.
23- 2	85	0.23	23-23	39	0.95
- 3	91	0.18	-24	87	0.14
- 7	36	1.50	-25	77	0.30
- 8	72	0.38	-28	86	0.18
-10	10	2.07	-29	87	0.18
-13	57	0.49	-30	85	0.20
-14	54	0.60	-31	96	0.05
-16	87	0.15	-32	88	0.19
-17	45	0.77	-36	84	0.19
-18	70	0.57	-37	97	0.03
-20	87	0.17	-40	86	0.20
-21	81	0.25	-41	89	0.12
-22	83	0.22	-42	91	0.11
$\bar{x}$				75	0.40
Parent Clone No. 23				87	0.13

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